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THE CRANE FLY GENUS *CHIONEA* IN NORTH AMERICA[1]

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Abstract

This is primarily a taxonomic revision; eight new species of nearctic *Chionea* are described: *durbini, excavata, hybrida, jellisoni, lyrata, nigra, obtusa* and *wilsoni*. *Chionea noveboracensis* Alexander is placed in synonymy of *C. valga* Harris. These changes result in recognition of 16 North American species. The earlier grouping of species based on number of flagellomeres is rejected, and three species groups based on genital and other characters of both sexes are recognized. Separation of *Niphadobata* Enderlein from *Chionea* is rejected.

Morphological adaptations of *Chionea* for loss of wings and a largely subterranean life are examined. External anatomy and internal anatomy of the adult flies are described. The eggs, larvae and pupae are briefly described, including internal anatomy of the larva.

Ecological relationships of *Chionea* to the physical environment and to other organisms are discussed. In particular, the temperature range within which *Chionea* is active on the snow and the flies' survival in extreme cold are explored. Various species of *Chionea* are shown to transport phoretic nematodes and to serve as intermediate hosts of mouse tapeworm. Geographic distribution of the species is correlated with latitude, elevation and plant cover.

Introduction

Among the more curious of the thousands of known species of Tipulidae are the little wingless snow flies that comprise the genus *Chionea*. Their peculiar, spider-like appearance and unusual occurrence as adults in winter have long made them subjects of comment by entomologists; however, the fact that they are abroad when most people are inclined to remain indoors has discouraged the collection of many specimens or of detailed information about their life histories and activities. Several species have been recognized and described, and occasional field observations of the living insects have been made, yet our fundamental knowledge of the genus remains fragmentary. Nearly every paper published on *Chionea* in North America has been based upon the chance discovery of one or two specimens; in fact it was precisely such a discovery of a mere five individuals that prompted my own investigation of these insects.

This study has been rather unsatisfying in certain respects, largely because of the difficulty of finding *Chionea* either alive in its natural surroundings or preserved in collections. Only about 1100 adult specimens could be brought together from all sources, and the distribution of these among the various species is extremely uneven. Moreover, I have rarely had the opportunity to observe living adults. The immature instars of *Chionea* have been encountered only two or three times in Europe, and only twice in North America. Because of this rarity of specimens, intraspecific variation has not been well understood in the past, with the result that the taxonomy of *Chionea* has been in certain instances confused. The long-standing misinterpretation of certain details of their external and internal anatomy may also be due to this rarity of specimens for study.

In view of these circumstances, it seems to me worthwhile to bring together and reorganize the accumulated facts about *Chionea*, adding to them such things as I have been able to learn about the morphology, natural history and taxonomy of the genus. Perhaps what follows also will serve to stimulate further interest in these flies, which may some day lead to a more complete treatment of them.

Acknowledgments

Several people have contributed to this undertaking in various ways, and the help of all is appreciated. For early encouragement in the study of *Chionea*, I am indebted to the late Prof. J. Speed Rogers of the Univ. of Michigan; and for helping in many ways, especially by making available the types of his species of *Chionea*, I thank Prof. Emeritus Charles P. Alexander of Amherst, Massachusetts. I am indebted to eight hardy entomologists, in particular, for making the major collections of *Chionea* studied: Dr. M. S. Briscoe, Howard Univ.; Dr. John A. Chapman, then of Montana State Univ.; Mr. David V. Durbin, San Francisco, California; Mr. Roger A. Haick, then of the Univ. of Montana; Dr. William L. Jellison, Hamilton, Montana, formerly of the Rocky Mountain Laboratory, U. S. Public Health Service; Dr. William S. Osburn, then of the Univ. of Colorado; Mr. David S. Potter, Univ. of Montana; and Mr. Gary A. Shook, Boise, Idaho. I wish to thank the following curators and others for the loan of specimens: William F. Barr, Univ. of Idaho; Sydney G. Cannings, Univ. of British Columbia; P. J. Darlington, Museum of Comparative Zoology, Harvard Univ.; Henry Dietrich and L. L. Pechuman, Cornell Univ.; Paul Freeman, British Museum (Natural History); Maurice T. James and William J. Turner, Washington State Univ.; Edward L. Kessel and Paul H. Arnaud, Jr., California Academy of Sciences; Hugo G. Rodeck, Univ. of Colorado; Herbert H. Ross and Donald W. Webb, Illinois State Natural History Survey; Herbert J. Teskey and Guy E. Shewell, Entomology Research Institute, Canada Department of Agriculture; Alan Stone, USDA, U. S. National Museum; and John A. Wilcox, New York State Museum. I am particularly grateful to Dr. Ryuichi Matsuda and Dr. Herbert J. Teskey for constructive criticism of respectively the morphological and all other parts of this paper. Finally, I thank all others who have sent specimens of *Chionea* during this study, for every specimen has been a substantial addition.

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The Genus Chionea

Chionea is a small genus of only about two dozen species, widely scattered about the Holarctic region, 16 occurring in North America and the others in Europe, far eastern U.S.S.R., and Japan. Although these species exhibit considerable variation in anatomical details, they have an overall similarity that involves a number of conspicuous specializations (such as extreme modification of the thorax), imparting to the genus the appearance of structural homogeneity and at the same time so setting it apart from other genera that it is not easy to conceive of a more "natural" group. In spite of this, the most recent revision of the European species (Burghele-Bălăcesco, 1969) recognizes separate genera, *Chionea* and *Niphadobata*, for species groups differing in structure of the aedeagus of the male and in details of the antennae. Enderlein (1936: 19) had based *Niphadobata* on the number of antennal segments (6-7, compared to 9-10 in typical *Chionea*). Kratochvil (1936: 250) found that most flagellomeres in the species with longer antennae (*longicornae* group) have four verticillar hairs while those in the other group (*brachycornae*) have three. He also noted that in the *longicornae* group the aedeagus is shorter than the gonapophyses and has small basal parameres, in contrast to the condition in the *brachycornae*, in which the aedeagus is longer than the gonapophyses and has no basal parameres.

Some North American species of *Chionea* bridge the gap in number of antennal segments, as discussed below, and the difference in number of verticillar hairs does not hold for our species. Three verticillar hairs is the usual number in nearctic species with short antennae, for example, *C. alexandriana*, which has three flagellomeres. But three is also the usual number in *C. scita* and *C. albertensis*, which have respectively eight and ten flagellomeres, on the average, and also in those species having an intermediate number of flagellomeres. The number of such hairs is not constant within a species, however, and one or two flagellomeres may have four hairs while others of the same antenna have three.

None of the nearctic species belongs to the typical European group on the basis of short aedeagus with basal finger-like parameres; thus, there is no correlation whatsoever of aedaegal structure with length of antennae. Furthermore, I am inclined to reject the division of *Chionea* into two genera on this basis because to do so ignores the great number of structural specializations of the thorax, legs, wings, halteres and abdomen that all the species have in common.

I have yet to see a key to the Diptera that will identify a specimen of *Chionea* as a tipulid. Its winglessness (actually it has tiny vestiges of wings) and stout body render it an unlikely candidate for offhand inclusion with other crane flies, and it lacks the V-shaped transverse mesonotal suture by which supposedly all Tipulidae may be known from similar flies in other families.[2] Its broad sternum separates the coxae widely, and when the antenna are greatly reduced, as happens in certain species, the inexperienced entomologist might suspect that *Chionea* belongs among the Pupipara. The genus was, in fact, placed in a separate family for a time during the middle 1800's by such eminent dipterists as Rondani, Zetterstedt and Bigot (e.g., Rondani, 1856: 38, 189). By 1869, however, Osten Sacken showed the eriopterine affinities of *Chionea* and moved the genus near to its currently accepted systematic position. Allowing for the moment that *Chionea* belongs somewhere among the Tipulidae, it must further be placed in the subfamily Limoniinae, on the basis of the short terminal segment of the maxillary palps and the structure of the ovipositor, which is unlike the form found in the Tipulinae or Cylindrotominae. The placement of the genus in the tribe Eriopterini is based upon the following combination of characters:

1. eyes without short hairs interspersed among the facets, such as are found in the Pediciini, some of which are wingless.
2. tibiae without spurs.
3. pretarsal claws not toothed.
4. empodia well developed in form of arolia.

Certain genera of the Eriopterini exhibit some of the unusual structural characteristics of *Chionea*, as, for example, the fusion segment at the base of the antennal flagellum or the undivided dististyles on the male genital segment. Accordingly, Alexander (1916: 530) regarded *Chionea* as a specialized relative of these genera, *Cladura* and *Pterochionea* (now regarded as a synonym of *Cladura*), in a subtribe later designated the Claduraria, to which group the European *Crypteria* and American *Neolimnophila* also belong. Subsequent comparison of the immature forms of *Chionea* and *Cladura* has strongly supported Alexander's placement of the genus near to *Cladura*.

NORTH AMERICAN CHIONEA

Although aware of some differences between Old World and American Chioneas, I do not believe the North American species can yet be distinguished as a group from their Eurasian relatives. I have studied the palearctic species only sufficiently to say that little more is known about them than about the American forms, except that their taxonomy has recently been revised in a detailed and excellently illustrated publication by Anca Burghele-Bălăcesco (1969).

Thirteen North American species of *Chionea* have been described: *C. alberten-*

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[2] Marchand (1917: 151) discovered an indication of taxonomic affinity that nearly everyone else seems to have overlooked: "One of the . . . specimens (of *Chionea*) . . . was found to have lost all its legs during transportation, showing . . . in this peculiarity its relationship to the Tipulids." See also Ainslie (1906).

sis Alexander, *C. alexandriana* Garrett, *C. aspera,* Walker, *C. carolus* Byers, *C. gracilis* Alexander, *C. macnabeana* Alexander, *C. nivicola* Doane, *C. noveboracensis* Alexander, *C. primitiva* Alexander, *C. scita* Walker, *C. stoneana* Alexander, *C. valga* Harris, and *C. waughi* Curran. *Chionea aspera* has long been recognized as a synonym of *C. valga,* and although *C. scita* was also regarded as a synonym of *valga* for many years (Alexander, 1942: 429) I have considered it a valid name, with *C. primitiva* its synonym (Byers, 1963: 160). On the basis of my opinions expressed in correspondence with him, Alexander (1965: 72) placed *C. gracilis* and *C. waughi* in the synonymy of *valga.* These rearrangements in the Catalog of the Diptera of America North of Mexico (Stone et al., 1965) should have been noted as new synonymy. I further regard *C. noveboracensis* as a synonym of *valga.* To the remaining list I shall here add eight previously undescribed species, bringing the total to 16.

Species heretofore described have been differentiated largely on the basis of color, size, and number of antennal segments. In the following revision, however, I shall try to show that these characters, while useful for the differentiation of species groups, have only limited utility in the diagnosis or recognition of the species. The most consistently useful characters for species recognition are the shapes of the gonapophyses in the male, and of the ovipositor and associated sclerites in the female; less commonly, another character may by some peculiarity prove to be wholly reliable.

Many tipulid genera have been divided into subgenera—a practice widely adopted in the taxonomy of nematocerous Diptera. Although this has not been done in the case of *Chionea,* two major species groups were proposed by Kratochvil (1936: 250) for the European species: *Chioneae longicornae,* including those species with nine or ten antennal segments; and *Chioneae brachycornae* (emended to *brachycerae* by Alexander, 1940: 101), including species that have six or seven antennomeres. Enderlein (1936: 19) gave the *brachycornae* generic status, as *Niphadobata,* but this name has not been consistently applied in the more recent literature (cf. Burghele-Bălăcesco, 1969). In classifying the North American Chioneas, Alexander (1941: 212) adopted species group names, respectively *araneoides* group for the *longicornae* and *valga* group for the *brachycerae.* While I have retained the *valga* group in my classification, it is based upon a combination of characters as set forth below. In the North American species there is continuous variation in number of antennal segments from four (i.e., scape, pedicel, fusion segment and one additional flagellomere) to 12, the number for any species varying often by one, rarely by two, exceptionally by more than two. I have therefore abandoned the older classification in favor of the following, applicable to the North American species only:

1. *scita* group—general body color yellowish brown or brown; antennae of 10-12 segments; gonapophyses of male bladelike, without upturned apical hook; eighth abdominal tergum of female short (much less than half length of seventh tergum, measured front to rear); includes *scita, albertensis, nivicola, wilsoni* n. sp., and *macnabeana.*

2. *valga* group—general body color reddish brown, grayish brown or dark brown; antennae of 5 (rarely 4) to 9 segments; gonapophyses of male in form of a horizontal blade with a vertical keel, without apical hook; eighth abdominal tergum of female longer, about half length of seventh tergum; includes *valga, stoneana, hybrida* n. sp., and *obtusa* n. sp. Inclusion of *stoneana* and *hybrida* here is based primarily on the structure of the gonapophyses. The other species as a group have 7-9 antennal segments, as contrasted with

4 or 5 in *stoneana* and *hybrida*, and the eighth tergum in females of *stoneana* and *hybrida* is lengthened only at the sides, appearing short in dorsal aspect.

3. *alexandriana* group—general body color light brown, brown, dark brown or black; antennae of 5 (rarely 4) to 7 segments; gonapophyses of male broad at base, slender, upturned and hook-like at apex; eighth abdominal tergum of female much shorter than half length of seventh tergum; includes *alexandriana*, *carolus*, *durbini* n. sp., *excavata* n. sp., *jellisoni* n. sp., *lyrata* n. sp., and *nigra* n. sp.

HISTORICAL REVIEW

The genus *Chionea* was established in 1816 by J. W. Dalman for a northern European species, *C. araneoides*, which is type species of the genus by monotypy. Thaddeus Harris described the first North American species, *C. valga*, in 1841, though as early as 1833 he had mentioned the occurrence of the genus in Massachusetts and in 1835 named the species without describing it. Two North American species were shortly afterward described by Francis Walker, *Chionea aspera* (a synonym of *valga*) and *C. scita* (Walker, 1848).

No additional North American species were discovered then for over 50 years. In 1900 R. W. Doane named the first species from western North America, *C. nivicola*. Charles P. Alexander in 1917 described *C. gracilis* and *C. noveboracensis* (both here regarded as synonyms of *valga*), and *C. primitiva* (a synonym of *scita*). C. B. D. Garrett named the second species from the West, *C. alexandriana*, in 1922; and in 1925 C. H. Curran described *C. waughi* (synonymous with *valga*).

Subsequent additions to the list of American species have been the work of C. P. Alexander and include *C. stoneana* (1940), *C. albertensis* (1941), and *C. macnabeana* (1946).

References to North American *Chionea*, other than these of a purely taxonomic nature, have been in general limited to a few brief notes on casual observations of the adults. Nothing has so far been published on the biology or life history of these flies except by John Chapman (1954: 360-363), who discussed the ecological and seasonal distribution of some western species and described their activities at various temperatures.

Mention should be made of the work of Jacques Bitsch (1955), which deals with European species but offers the only modern treatment of the external anatomy of *Chionea*, and of Anca Burghele-Bălăcesco (1969), concerning taxonomy of the European species based upon careful study of the genitalic anatomy.

Because of its extreme structural modification, *Chionea* has been accorded varying degrees of special taxonomic status by various dipterists. Rondani (1841: 284) early regarded it as in a separate "familia," Chioneinae, and Zetterstedt (1842: 104) gave the genus apparent family status as Chioneides. Bigot (1854: 466) also placed the genus in a separate family, Chioneidae. However, Osten Sacken (1869: 136) noted the many similarities between *Chionea* and certain other crane flies and arranged it with the Eriopterina (now tribe Eriopterini), where it remains today. More recently, nevertheless, Williston (1908: 86) separated all the Limnobiinae (now Limoniinae) into tribes, except for *Chionea*, left standing alone as a genus. Burghele-Bălăcesco (1969) recognized two genera, *Chionea* and *Niphadobata*, for the European species, following Enderlein (1936) but with firmer morphological basis.

MATERIALS AND METHODS

Taxonomic and morphological descriptions which follow are based upon the study of somewhat over 1100 specimens of adults of *Chionea*—all that could be located by a fairly thorough search of mu-

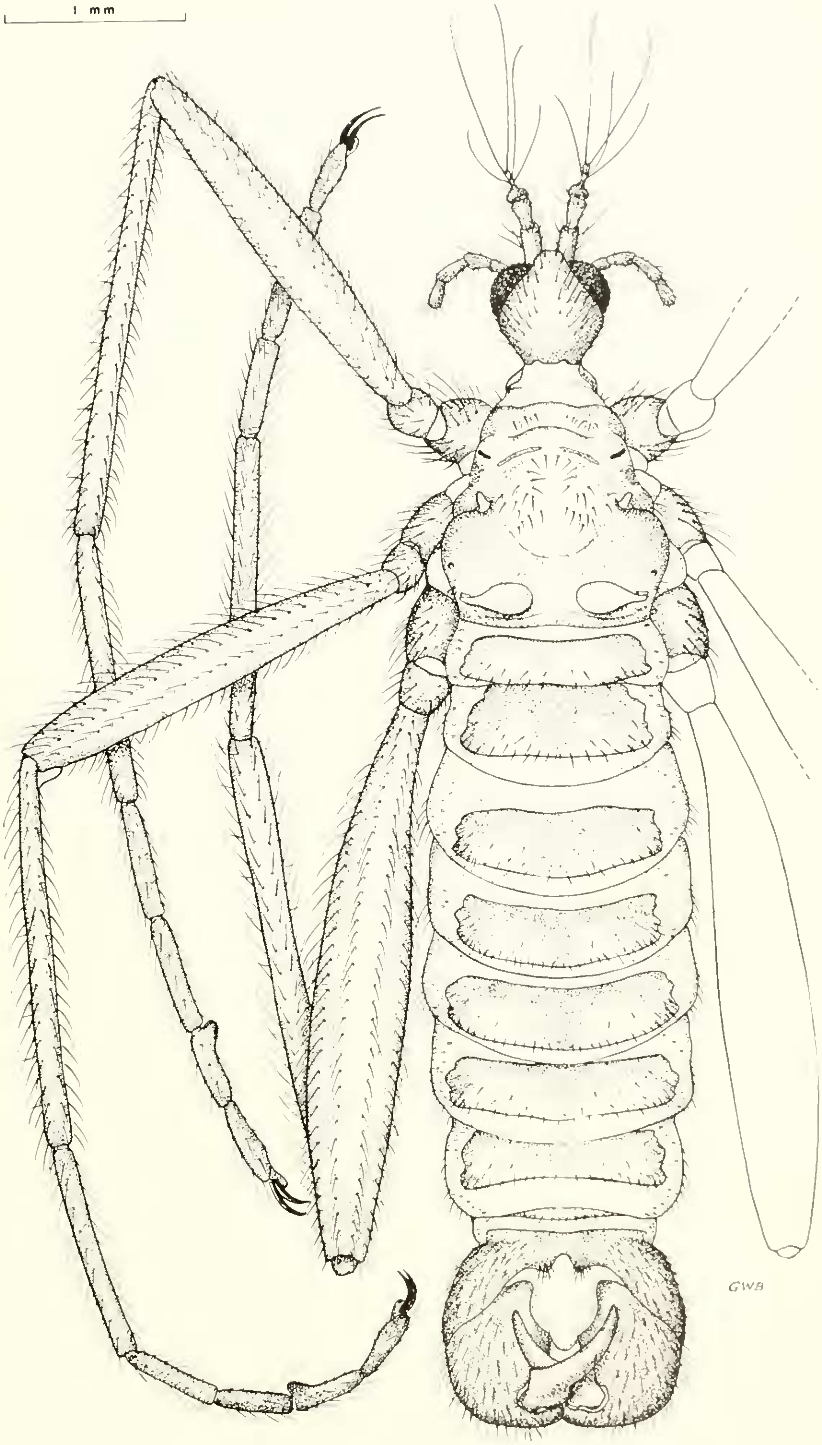


FIG. 1. *Chionea alexandriana* Garrett, male, dorsal aspect (most of right legs omitted), to show general habitus.

seums and other collections. These have included the holotypes or type series of all species except *C. noveboracensis* (type lost) and *C. alexandriana* (paratypes seen). The only immature forms studied were those of *Chionea valga* and *C. stoneana*. These will be described in detail in a separate paper, and only the latter are dealt with here in a general way.

Although numerous flies pinned dry have been seen, a greater number have been preserved in alcohol, the latter by far the more satisfactory specimens. Chioneas generally make pretty wretched pinned specimens because of their small size and tendency to become shriveled and distorted when dried, such as in extreme telescoping of the abdominal segments. Not only does preservation in fluid keep the insects in more or less their original shape and dimensions, but it also permits subsequent study of the internal structures and greatly facilitates identification, for the gonapophyses of the male are readily exposed by pressing the membranous tenth abdominal segment forward beneath the ninth tergum, and the ovipositor of the female is easily opened to reveal the shape of the ninth abdominal sternum and the genital furca.

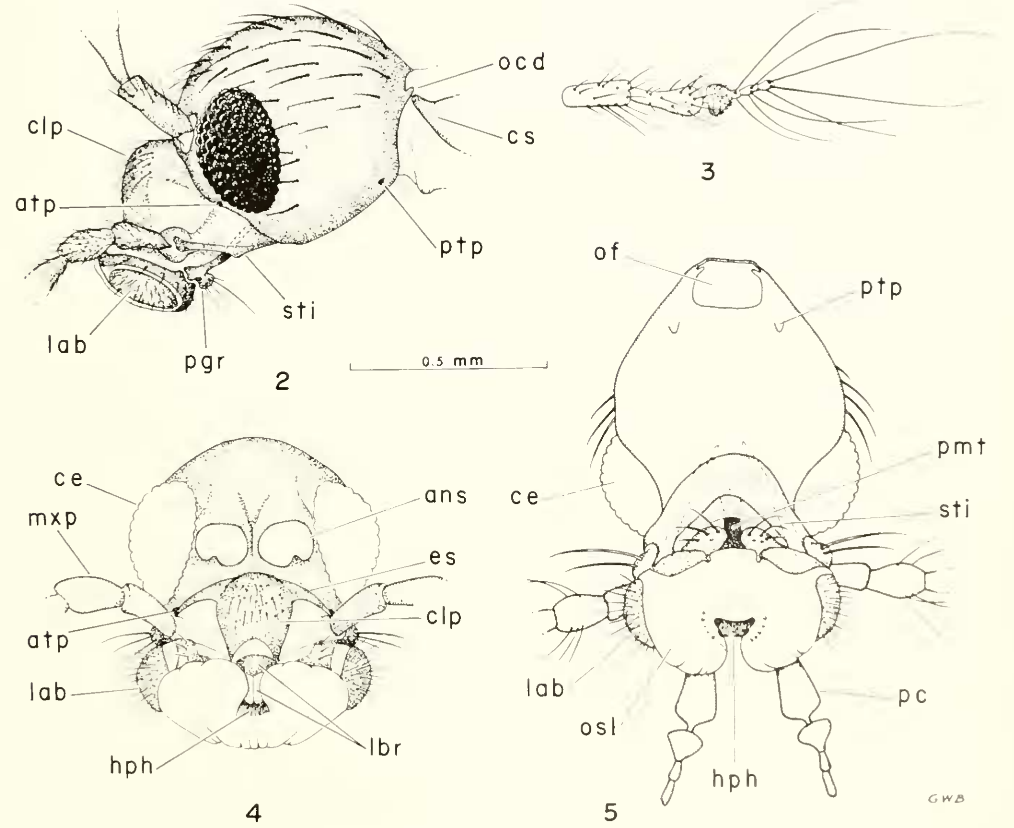
Specimens mounted on microscope slides were first cleared in 10% potassium hydroxide, then washed in increasing concentrations of ethyl alcohol (80%, 95%, absolute), then in xylene, and finally cleared somewhat further in clove oil. All were examined "in the round" before being mounted in Euparal medium.

Morphological studies were based upon flies preserved in 70-80% ethyl alcohol. There are, of course, better fixing solutions for muscle and internal organs, but alcohol suffices; besides, few Chioneas have ever been collected specifically for morphological examination.

Adults—External Morphology

General Description.—Being wingless and hairy and having a short body (Fig. 1) and short, stout legs (as compared to those of other tipulids), flies of the genus *Chionea*, when seen from a few feet away, superficially resemble spiders, a similarity suggested in the name of a European species, *C. araneoides*. They are small crane flies, their overall length, exclusive of the antennae, varying from about 3-8 mm, depending in part upon the species and the degree of abdominal contraction ("telescoping"), which is in turn dependent upon whether the insect is alive or not and if preserved whether dried or in fluid. There is also extensive size variation among individuals of the same species similarly preserved, as will be discussed later. General body coloration varies from pale to dark yellowish brown through reddish or grayish brown and dark brown to black but is fairly constant within a species; callow individuals are always somewhat paler than more fully matured adults.

Head.—Several structural details of the head of *Chionea* differ noticeably from their counterparts in other crane flies, the most striking being the antennae, which consist of scape, pedicel and a variable number of flagellomeres. The nearly cylindrical scape bears a few scattered setae on its dorsal surface, fewer or none ventrally, before an irregular subapical whorl (Figs. 2, 3). Subequal in length to the scape, the peculiarly elongated pedicel is narrowed at its base but expanded in the distal half; it bears a fairly distinct verticil of 10-12 setae slightly before the segment begins to narrow toward the flagellar attachment and a scattering of other setae in no apparent pattern. While the number of flagellomeres is rather constant in most tipulid genera, it varies at least from 2-10, mostly according to species, in *Chionea*. This, of course, attracted the attention of taxonomists long ago and understandably became one of the first criteria for species recognition. The first flagellar "segment" is much thicker than the others and has a subconical or turbinate shape (Fig. 3), while the second and succeeding segments are elongate and of more uniform diameter. Since among the Eriopterini in general the number of flagellomeres is 14, the enlarged first segment in *Chionea* is judged to have originated by fusion of some greater number of segments, varying 5-13 as the number of segments beyond it diminishes correspondingly from 9-1. This first segment is accordingly known as the fusion segment, and although it cannot clearly be seen to comprise more than one segment in *Chionea* (but see C. W. Johnson's comment in Alexander, 1917: 202), its structure in the closely allied *Cladura* (formerly *Pterochionea*) *bradleyi* (Alexander), showing five distinct verticils, seems to substantiate this interpretation. I have compared the antennae of *Chionea scita* and *Cladura bradleyi* (as *Pterochionea*) in another paper (Byers, 1961*a*: 190-191). The fusion segment is densely pitted and clothed with short hairs except on its base. Occasionally, especially in species of the *alexandriana* group in which there is greatest reduction of the antennae, there will be found a long seta or two attached near the apex of the fusion segment. In the *scita* group the second flagellomere (first beyond the fusion segment) is covered



Figs. 2-5. *Chionea alexandriana*, details of head. 2, head, left lateral aspect. 3, right antenna, dorsolateral aspect. 4, head, frontal or facial aspect (antennae removed). 5, head, ventral aspect. Abbreviations: ans—antennal socket, atp—anterior tentorial pit, ce—compound eye, clp—clypeus, cs—cervical sclerite, es—epistomal suture (sulcus), hph—hypopharynx, lab—labial palp, or labellum, lbr—labrum, mxp—maxillary palp, ocd—occipital condyle, of—occipital foramen, osl—oral surface of labellum, pc—pedicel of antenna, pgr—palpiger of labial palp, pmt—prementum, ptp—posterior tentorial pit, sti—stipes of maxilla.

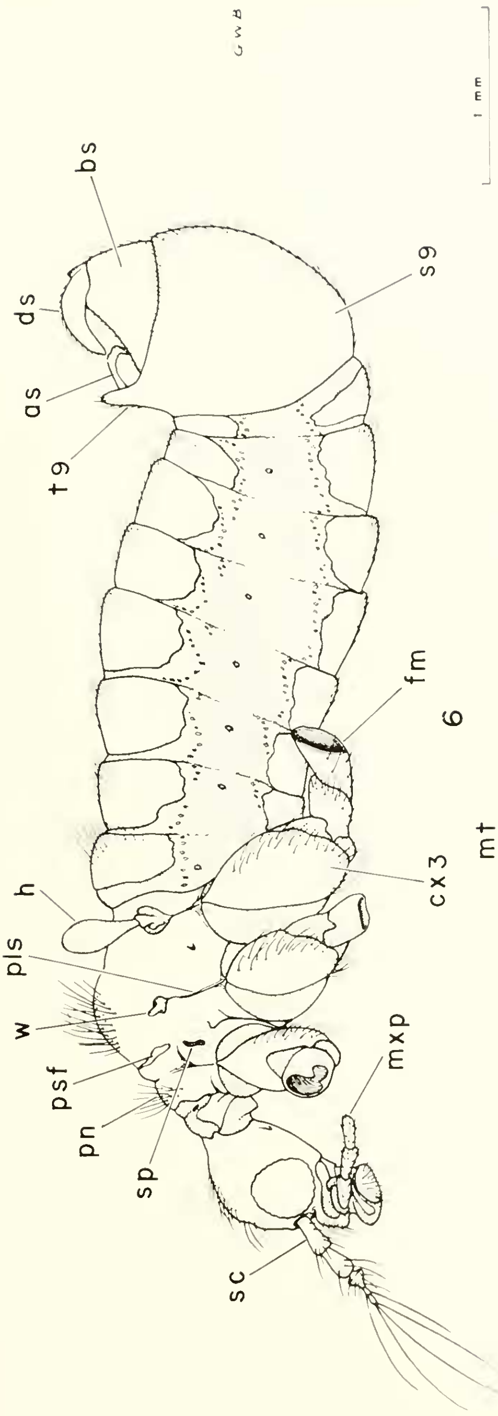
with short hairs similar to those of the fusion segment. The other flagellomeres have three, or rarely four, long setae arranged in irregular whorls. In general, these verticils increase in length as the number of flagellomeres is reduced, as if to compensate for the reduction and maintain antennal length (e.g., compare Fig. 3 with 97). This may be an instance of what Matsuda (1979: 220) has called material compensation, such compensatory development often being seen in insects with reduced wings (p. 224).

The compound eyes are black in the living flies and often retain this color in preserved specimens. They are composed of about 80-200 ommatidia, the number varying generally according to species but also somewhat among individuals within a species, without any evident sexual dimorphism. They occupy a comparatively smaller portion of the head surface than in most Tipulidae, a reduction in size that may be related to the largely subterranean habits of *Chionea*. It has been observed that subterranean and cavernicolous insects often have not only smaller compound eyes than their nearest relatives living above ground but also larger ommatidia, which perhaps are more efficient in gathering light in parts of the environment where some light is available. To see how this might apply in the case of *Chionea*, I compared the compound eyes of male specimens of *Chionea valga* and the related *Cladura flavoferruginea* of approximately equal body size and head dimensions. In the slightly larger eye of *Chionea* there were nine facets (3 × 3) within a sample unit square, whereas the *Cladura* had 16 (4 × 4), a 78% greater number of ommatidia per unit area in the day-flying *Cladura*. The size and number of ommatidia in most other species of *Chionea* are rather close to those in *C. valga*. Ability to perceive form clearly, it seems, would be of little use to a slowly moving, non-flying insect such as *Chionea;* on the other hand, living as it does in darkened recesses beneath the ground and coming onto the surface primarily at times of low light intensity, it would derive some benefit from eyes adapted to making the most of what light there was.

Surface areas of the head such as genae, frons, vertex and occiput are indistinguishably fused, the only useful "landmarks" other than eyes and antennae being the tentorial pits, of which the posterior pair may easily be seen at about 125× magnification (Figs. 2, 5). The anterior tentorial pits (Fig. 4) are smaller and concealed in the epistomal (fronto-clypeal) suture, close beneath the eyes. The vertex bears a group of stout hairs, the longer ones of which are subequal in length to the scape.

The short, thick rostrum is made up of the strongly arched clypeus in front and a posterior (ventral) sclerotized area in which the stipites of the maxillae are embedded (Fig. 2) and which is slightly inserted under the antero-ventral margin of the head, to which it has a membranous connection. Although joined by this sclerotization, the stipites are not fused medially as in tipuline crane flies, such as *Dolichopeza* (Byers, 1961*b*: 684, Fig. 9). Except for the stipes, the maxilla consists only of a five-segmented palp, of which the first segment is approximately spherical, the second elongate and somewhat curved, the third enlarged and having a more roughly

Figs. 6, 7. *Chionea alexandriana,* external anatomy. 6, adult male, left lateral aspect (legs mostly omitted); as—anal (tenth) segment, bs—basistyle, cx3—coxa of metathorax, ds—dististyle, fm—femur (cut shortly beyond trochanter), h—haltere, mxp—maxillary palp, pls—pleural suture of mesothorax, pn—pronotum, psf—pseudosutural fovea, sc—scape of antenna, sp—spiracle (of mesothorax), s9—ninth abdominal sternum, t9—ninth abdominal tergum, w—wing rudiment. 7, adult female, right lateral aspect (legs mostly omitted); ce—compound eye, cr—cercus, cs—cervical sclerite, hv—hypovalve, ms—microsternite, mt—microtergite, sp—spiracle (of metathorax), s1—first abdominal sternum, s8—eighth abdominal sternum, t8, t9, t10—eighth, ninth and tenth abdominal terga.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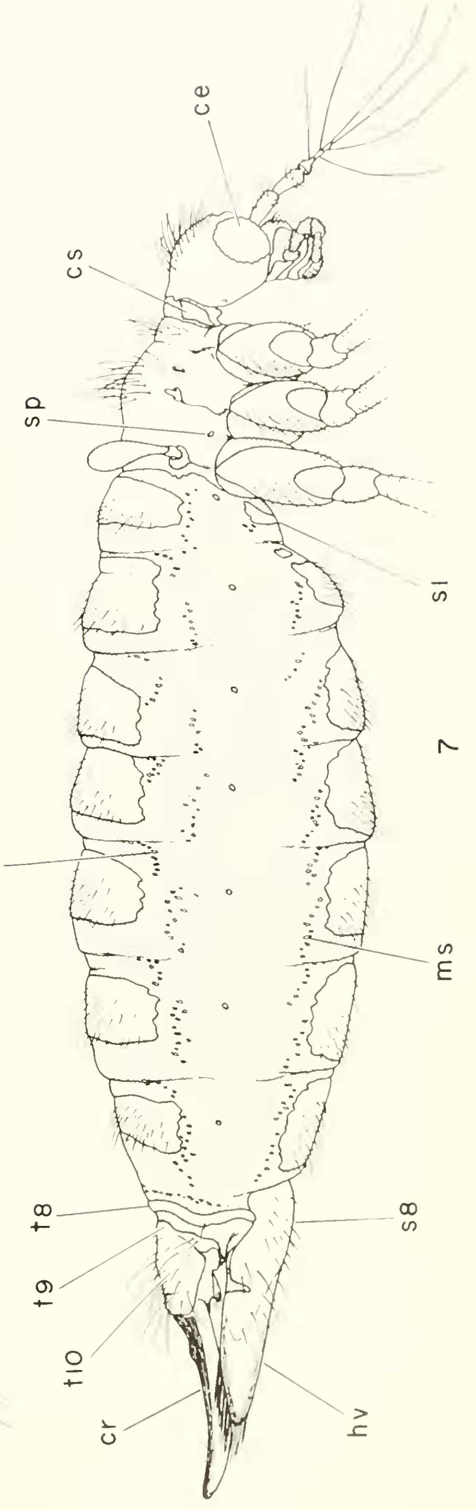
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t8
s8
t9
t10
cr
hv

7

pitted surface (sensory structures?) than the others, and the fourth and fifth segments more elongate, as shown in Figures 2 and 6.

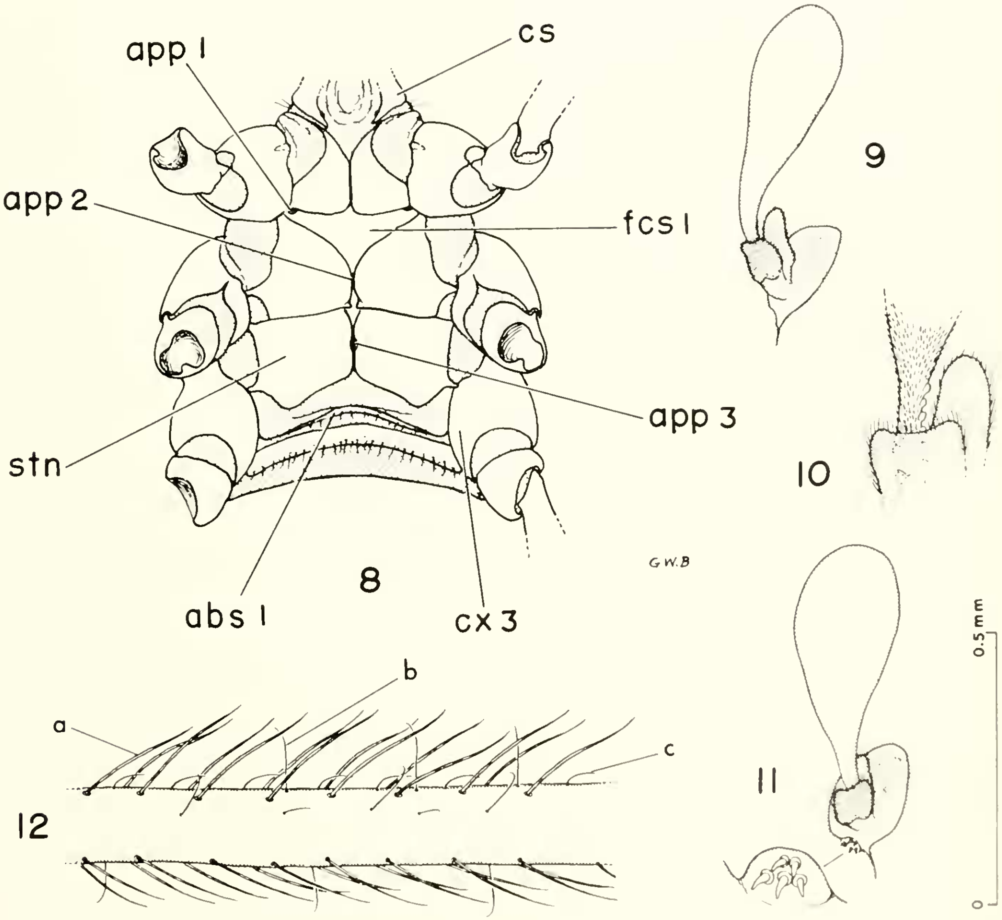
Partially telescoped beneath the maxillary bases is the strongly sclerotized prementun of the labium. It is forked at its inner (proximal) end, which extends into the head as an apodeme, and is slightly expanded distally where it adjoins directly the bases of the first labellar segments (Fig. 5). Over this junction lies a slightly sclerotized, setiferous lobe which I take to be a modification of the sclerite that in Tipulinae is interposed between the prementum and the first labellar segment. This sclerite has been called the palpiger by Rees and Ferris (1939: 147, Fig. 73) and, where divided, the "kappa" and "sigma" sclerites by Peterson (1916: 45-46, Plate XVII, Fig. 288). The labellar lobes are broad and dorsally clearly show division into two segments. Their ventral surfaces are remarkable in being quite smooth; that is, there are no pseudotracheae whatsoever (Fig. 5). At high magnifications, a row of tiny denticles can be seen near the meso-ventral margin of each lobe. These possibly are the equivalent of the prestomal teeth of certain higher Diptera (cf. Crampton, 1942: 36). The number of these denticles varies from 4-15, generally according to species, although it is not constant within a species. Closely appressed to the dorsal surface of the labium, in the deep notch between the labella, is the hypopharynx, which in *Chionea* extends far beyond the short labrum and, in the absence of labellar pseudotracheae, probably is used to take up liquid nutriment directly. The hypopharynx may be recognized by the compact brush of fine, golden hairs at its tip.

Thorax.—Loss of wings in *Chionea* has resulted in a corresponding diminution of the mesothorax, which, however, is still the largest thoracic segment. Wide and rather flat on the ventral side, the thorax is narrowed and arched above as shown by serial cross sections (Fig. 13, 14, 15) and increases in breadth from front to rear.

Since students of insect morphology cannot themselves agree on the interpretation of the thoracic sclerites, perhaps a mere taxonomist will be excused for making a somewhat arbitrary selection from among the available names for parts. Identification of thoracic areas in *Chionea* is complicated by the extensive fusion of dorsal and lateral sclerites and obliteration of many of the sutures that are fairly easy to discern in other tipulids. Using the coxae as reference points, however, it is not difficult to distinguish the three pleural sutures (Fig. 6, pls). The first of these (prothoracic) is in alignment with the junction between pronotum and mesonotum and terminates dorsally in a deep impression, which internally is the attachment of the sternal apophysis; and the second and third extend from the mesothoracic and metathoracic coxal processes, respectively, to the membranous areas about the bases of the vestigial wing and the haltere. Sclerotized areas before and behind these sutures may be identified as episternal and epimeral, respectively, but have no definite subdivisions (anepisternum, katepisternum, etc.), such as may be seen in the nearest relatives of *Chionea.* Crampton (1925: 201, 203) has commented on the reduction in *Chionea* of the mesothoracic meron, which in other genera of Eriopterini is large.

The pronotum, separated from the mesonotum by a fairly distinct suture, is crossed from side to side by an indistinct row of bristles. Two transverse, shallowly impressed, darkened spots on the mesonotum just above the slit-like mesothoracic spiracles (Fig. 6) appear to be the pseudosutural foveae. There is no differentiation of mesonotal prescutum, scutum, or scutellum, and the separation of mesothorax from metathorax is only weakly indicated dorsally by a shallow, transverse indentation and laterally by the position of the round metathoracic spiracles. Likewise, the nota grade imperceptibly into the pleural sclerites along the entire length of the thorax, the extensive, membranous paratergal areas seen in other tipulid genera being absent altogether (cf. Byers, 1961*b*: 687, Fig. 14).

In most crane flies, *Gnophomyia* being one exception, the coxae are set close together ventrally, and the mesosternum and metasternum are almost wholly infolded. By contrast, there are relatively broad ventral sclerites in *Chionea;* but the question arises—what is their identity? Are the sternal apophyses of the pterothorax ". . . carried inward upon a median inflection of the sternum to form the Y-shaped endosternal apodeme . . ." as stated by Snodgrass (1935: 171), or is it true that, as countered by Ferris (Rees and Ferris, 1939: 149), ". . . there is absolutely no sternal element visible externally on the thorax of any Dipteran . . ."



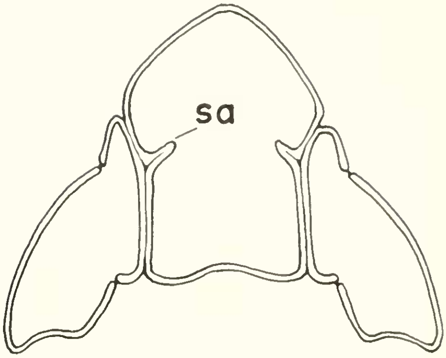
Figs. 8-12, *Chionea alexandriana*, details of thorax. 8, thoracic venter (legs mostly omitted): abs1—first abdominal sternum, app1—apophyseal pit of prosternum, app2—apophyseal pit of mesosternal furca, app3—apophyseal pit of metasternal furca, cs—cervical sclerite, cx3—coxa of metathorax, fcs1—furcasternum of prothorax, stn—sternum (combined basisternum and furcasternum) of metathorax. 9, haltere, posterior aspect. 10, detail of base of haltere, to show probable sensory structures. 11, haltere, lateral aspect; area of sensory pegs greatly enlarged. 12, *Chionea stoneana*, female, portion of hind tibia showing three kinds of setae (see text for explanation). Scale: Figs. 9, 11.

and that the apparent sternum is actually the subcoxal portion of the generalized insect leg, the endosternal apophyses (branches of the Y-shaped apodeme) being all that remain of the true sternum? It seems to me that Snodgrass and Ferris are in agreement that the ventral condyles articulating with the coxae belong to the subcoxal ring and that the sternal apophyses belong to the true sternum, so that what they are disputing is the location of the line of fusion between these two sclerites (cf. Snodgrass, 1935: 169, Fig. B, and Rees and Ferris, 1939: 165, Fig. 80c). In the cleared specimens of *Chionea* I have examined, as apparently also in many other Diptera, the line of fusion is not visible, its position therefore being hypothetical; consequently, there seems little to be gained by the argument. Rees and Ferris concede that what appears to be prosternum in *Tipula* is in fact the prosternum. If the same point of view is accepted for *Chionea,* then I would say that on the basis of structural similarity (Fig. 8) the meso- and metathoracic ventral sclerites are also sternal and that the Y-shaped sternal apophyses have been formed in these segments by the reduction of the furcasterna toward the ventral midline.

It is problematical why, in a dipteran that is altogether flightless, the halteres should be so well developed, but neither observation of the living flies nor microscopic examination of the structure of the halteres has led to an explanation. Except for the basal portion, or scabellum, the haltere is membranous and bladder-like (Figs. 9, 11) and covered with extremely fine hairs. The pedicel and capitellum, or knob, are not clearly divided. The capitellum seems to be hollow and in the living fly is probably filled with haemolymph. The scabellum comprises an incomplete cup, curving around the pedicel ventrally, and a longer dorsal lobe, both merging proximally on a slender, membranous attachment without any evidence of axillary sclerites. It is likely that the halteres in *Chionea* have some sensory function, for each has a fairly conspicuous nerve leading to it (but no visible tracheole), and on the base of the pedicel, mostly concealed within the scabellum, there are a dorsal and a ventral row of nodules, variable in number but most numerous dorsally, which probably are groups of sensilla (Fig. 10). There is also, at the edge of the episternum adjacent to the base of the haltere, a small swelling bearing a cluster of what appear to be sensory pegs (Fig. 11). It would seem that some movement of the halteres is involved in the stimulation of such sensory areas, but living Chioneas observed in the laboratory did not move the halteres noticeably, although, as will be discussed later, each has a small depressor muscle at its base.

Little need be said about the vestigial wings (Figs. 6, 7). They are shorter than the scabellum of the haltere, slender, and completely membranous, without setae or any other trace of venation. Like the halteres, they appear to be hollow and to contain haemolymph; and they seem to be quite immovable.

The legs in *Chionea,* especially the coxae and femora, are stout as compared to those of other eriopterine crane flies. It may be seen in Figures 6 and 8 that the laterally projecting coxae are hinged on pleural and sternal condyles but that the extensive membranous areas about their bases allow them to turn in a wide arc, providing the freedom of movement required for an altogether pedestrian insect. In females and small males the femora are only slightly incrassate, but in the larger, more robust males they are not only of increased length but also of disproportionately greater thickness. For example, among specimens of *C. valga* collected at the same place on the same day, a representative small male had an overall body length (from antennal bases to tip of abdomen) of 3.3 mm, a large one, 4.7 mm, a ratio of 1 to 1.42; length of hind femur increased by a ratio of 1 to 1.76, while greatest width of the femur increased by a ratio of 1 to 2.00. At the same time tibial length increased only proportionately, at a ratio of 1 to 1.41. These specimens were preserved in alcohol, so non-uniform telescoping of abdominal segments was not a major factor in body measurement. (A similar example of disproportionate variation is described later, under *Chionea obtusa.*) Seen from the side, the femora are almost straight along the ventral edge but broadly arched dorsally, and near the base they are curved slightly outward from the body. This combination is what led Harris to name his species *valga* (i.e., "bowlegged"). The tibiae are more or less straight and of uniform diameter throughout, except that at the proximal end, or head, they are slightly narrowed and sufficiently curved to allow them to close against the femora. There are no tibial spurs, as in Eriopterini generally. Each of the first three tarsomeres is cylindrical, the basitarsus about equal in length to the succeeding four segments together and the second longer than the third (Fig. 1). In females the fourth segment has more or less the same shape as the third, but in males it has a hairy basal enlargement on the ventral surface (Figs. 1, 36). I have not been able to discover any functional significance of this lobe. The terminal segment is narrowed at its base and a little enlarged apically, bearing a pretarsus with two untoothed claws and an almost transparent, bladder-like arolium. While the basitarsus has an indistinctly dicondylic attachment to the tibia, all the other tarsal joints are formed by a single dorsal condyle



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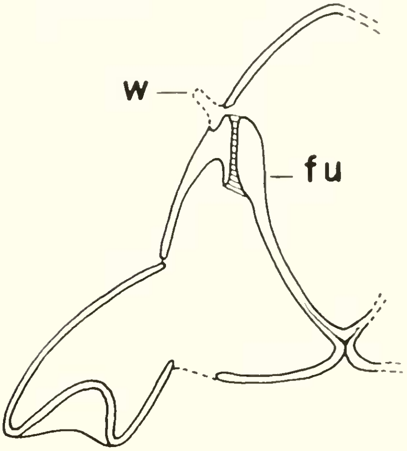

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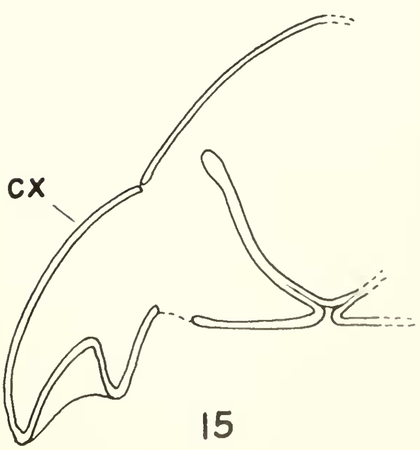

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FIGS. 13-15, *Chionea alexandriana,* cross-sections of thorax. 13, prothorax, at level of widely separated sternal apophyses (sa). 14, mesothorax, at level of wing (w), furca (fu) and pleural apophysis (joined to furca just below wing). 15, metathorax, at level of furca; cx—coxa.

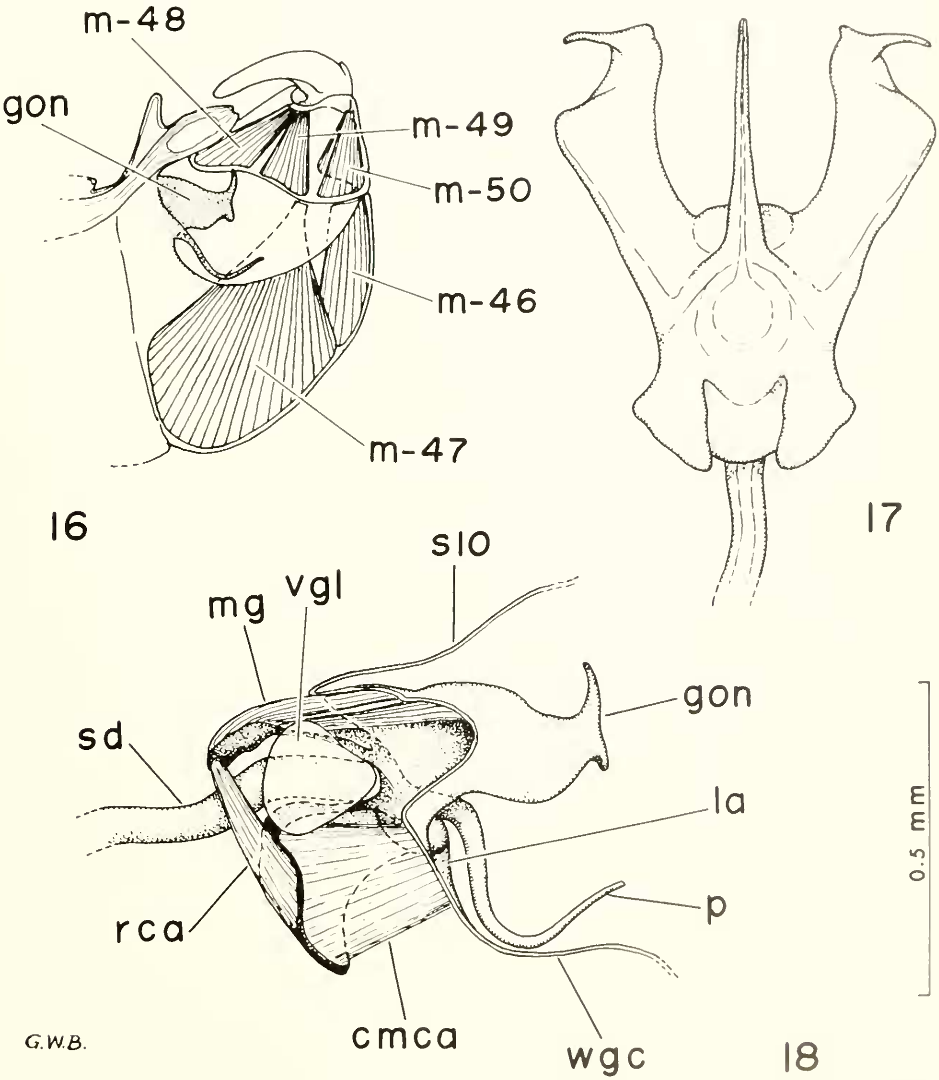
inserted into a socket in the preceding segment.

All the leg segments are sparsely covered with long, usually stout hairs or setae (Fig. 12, a), which on the femora and tibiae of most species are set in a variable number (e.g., 6-11 on the femora) of more or less definite but irregularly spaced, longitudinal rows. In most species the setae of the femora and tibiae are extremely attenuate and curved back at the tips (Fig. 12), and those on the dorsal surface are longer and less depressed than those on the ventral parts of the leg. In addition to these stout setae, there are slender, erect hairs (Fig. 12, b) occurring sparsely in a dorsal, ventral and two lateral rows, in which rows there also occur short, slender, strongly-decurved hairs (Fig. 12, c). The setae are long and thin in *C. valga* and the rows usually indistinct, giving this species a somewhat fuzzy appearance at low magnifications. In *C. stoneana,* likewise, the setae do not occur in distinct longitudinal rows. This species is different from the others in having the leg setae, most conspicuously those of femora and tibiae, short, each arising from a low, rounded papilla.

On the anterodorsal surface of each trochanter there is an oval, slightly elevated pad beset with fine, stiff hairs, each arising from a tiny pit. And on the ventral side of the femur, near the base, there is a rugose area containing shallow, oval depressions. These two modifications of leg segments are probably sensory.

Abdomen.—In both males and females the abdomen is largely membranous, with extensive pleural areas and with the sclerites widely separated. This is most noticeable in distended specimens such as those preserved in alcohol, but even when the insects are dried the pleural membrane bulges outward in conspicuous folds. When specimens are preserved dried, also, the abdomen contracts or telescopes so much that entire segments are likely to become concealed. Thus, Doane (1900: 189) described the female of *Chionea nivicola* as having a total of only six abdominal segments; and the number of segments before the enlarged ninth, or genital, segment in the male, accurately shown for *C. valga* by J. H. Emerton (Johnson, 1907: 43), was illustrated as seven in *C. alpina* by Marchand (1917: Fig. 1) and as six in *C. gracilis* and only four in *C. primitiva* by Alexander (1917: Figs. 1, 2). There is little modification of the first eight abdominal segments in the male or of the first seven in the female, except that the first sternum is very short (that is, a slender, transverse sclerite somewhat expanded at its ends) and the second sternum usually has a small, wedge-shaped sternite anteriorly at each side (Fig. 7). Spiracles occur on the first seven segments in both sexes. The terga and sterna are sparsely hairy and the terga especially may show an indistinct pattern of coloration (Fig. 1). The membrane appears smooth at magnifications up to 120×, but closer examination with the compound microscope reveals tiny subcircular patches of a few hairs each. Embedded in the membrane and distributed along the edges of the terga and sterna and in thin transverse lines dorsally between the terga and ventrally between the sterna (Figs. 6, 7) are a number of minute smooth, oblong, sclerites of various dimensions; these serve for muscle attachment, as will be discussed later. It seems appropriate to refer to these as microtergites and microsternites.

Modification of the abdomen in the male begins with the very strongly sclerotized ninth segment, the tergum and sternum of which are solidly fused into a continuous ring, which is prolonged ventrally beneath the thick basistyles (Fig. 6). Seen from above, the posterior margin of the ninth tergum appears either broadly and evenly emarginate (as in *C. valga*) or entire (as in *scita*), or it may be more distinctly, even narrowly, indented with blunt or projecting setiferous lobes at either side of the emargination (as in *albertensis*). The basistyles are separated from the sternum and are freely movable. Completely sclerotized mesally as well as laterally, the basistyles have roughly the shape of truncate cones but are somewhat curved inwardly at their apices. They bear long setae on their outer surfaces but shorter, more slender hairs on the mesal surfaces. On the inner posteroventral surface of each there is a thickened, blunt protuberance (Figs. 145, 146, 165, 175), often comprising two rounded lobes, densely covered with short,



FIGS. 16-18, *Chionea alexandriana*, details of male genital structures. 16, composite longitudinal section through ninth abdominal segment to show musculature of basistyle and dististyle: gon—gonapophysis, m—muscle (see text for origins, insertions and actions of numbered muscles). 17, gonapophyses, vesica, penis and anterior seminal duct, dorsal aspect. 18, genital structures, to show musculature: cmca—compressor muscle of compressor apodeme, gon—right gonapophysis, la—lateral apodeme, mg—muscle of gonapophysis, p—penis, rca—retractor muscle of compressor apodeme, sd—seminal duct, s10—tenth sternum (membranous anal segment), vgl—vesicular gland, wgc—wall of genital chamber (membranous). Scale: Fig. 18.

fine hairs. Each basistyle bears a single elongate, rigidly sclerotized dististyle, rather finger-like in general aspect. It is thickest and irregularly shaped at the base and usually more or less evenly curved and somewhat tapered toward the apex. There is a prominent, sometimes darkened, posteromesal tooth near the base (Figs. 155, 184), also a very small, inconspicuous, anteromesal tooth and an additional blackened ventral tooth of variable shape and size, most conspicuous in larger males, often rudimentary in smaller males and apparently invariably absent in certain species. The dististyle is sparsely covered with setae along its outer (dorsal) surface but is bare on its inner curvature, except for a small patch of stiff hairs near the base.

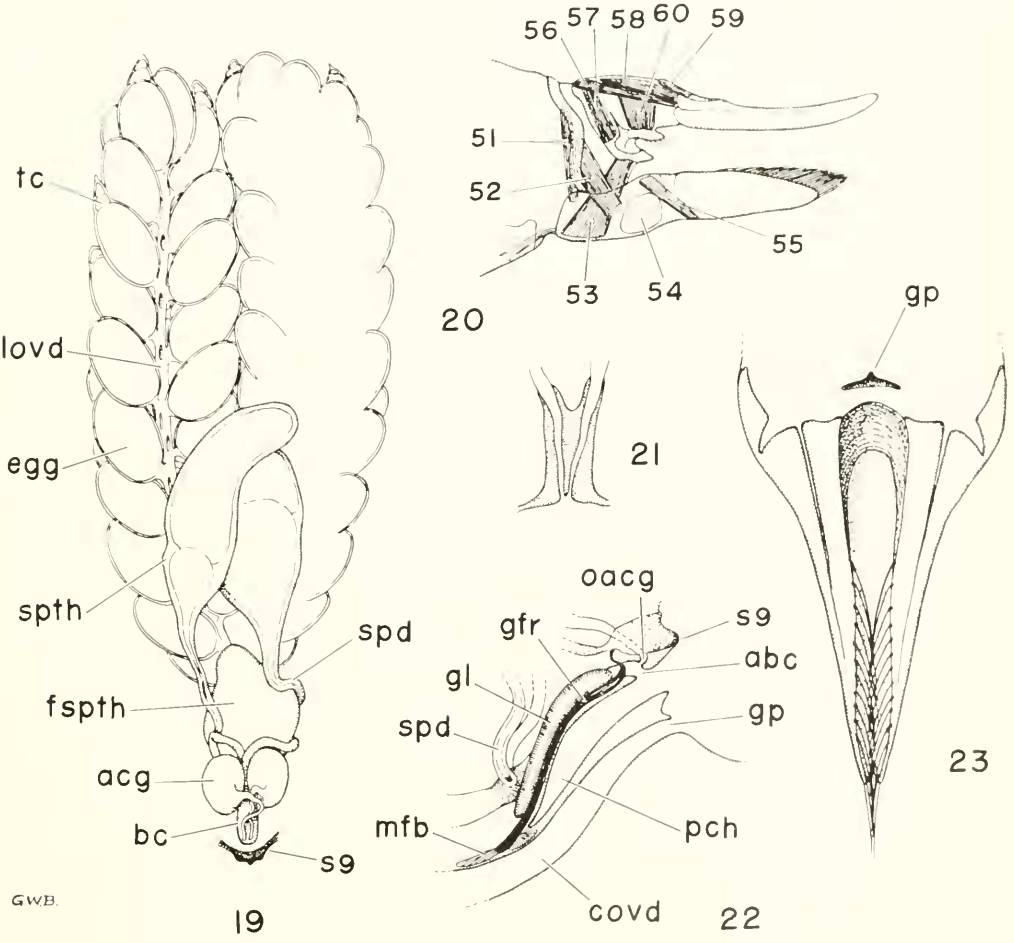
Ordinarily the gonapophyses (cf. Crampton, 1942: 92) are not easy to see because they are concealed from below and behind by the ninth sternum and basistyles and from above by the membranous tenth segment (Fig. 16). However, with the tip of a needle the tenth segment may, in a softened specimen, be pushed forward beneath the ninth, exposing the gonapophyses. Since this is the way they are most readily seen, I have illustrated the dorsal aspect for each species in the taxonomic treatment which follows. The gonapophyses are hardened and may be blade-like or hooked at the tip, as briefly discussed earlier, but they are hollow basally, where they are immovably fused to the sclerotized wall of the genital chamber and more flexibly attached laterally to the underside of the ninth tergum where it adjoins the basistyles (Fig. 18). These projections in *Chionea* could be described morphologically as parameres and probably are not homologous with the gonapophyses of some other tipulids, *Dolichopeza* for example (Byers, 1961*b*: 688); however, I am retaining the term because of its past use in taxonomy and because the structures seem to conform to a general definition of gonapophyses.

Emerging through the anterior wall of the genital chamber between the bases of the gonapophyses, the penis, a short, nonextensible intromittent organ, curves downward to the floor of the genital chamber and then upward again (Fig. 18). In most species the distal end of the penis is unmodified, but in *C. albertensis* it is produced into two sharp points and in *C. valga* and *C. obtusa* into two sinuate flagella; in *C. scita* there is a spoon-shaped extension at the tip.

Behind the ninth segment, or hypopygium, there is only the membranous tenth, or anal, segment. It could be argued that morphologically this must be the fused tenth and eleventh segments, but in *Chionea* there is no indication of a division into two parts. In some species the sides of this segment are pigmented and lightly sclerotized (Fig. 6).

In the female the eighth and succeeding abdominal segments are modified for copulation and oviposition. Elsewhere (Byers, 1961*b*: 690-692), I have compared the tipulid ovipositor in some detail with that of a typical pterygote insect, and since the female terminalia in *Chionea* do not differ greatly from those of a tipuline crane fly, the comparison need not be repeated here. Unlike the terga before it, the eighth tergum extends completely across the pleuron, and although it is not fused with the eighth sternum the two are joined by a strong, flexible attachment. In all species the eighth tergum is very short, about half the length of the seventh in some species (Figs. 112, 147) and reduced to a slender, transverse strap (Fig. 7) in others. It is bare except for one or a few hairs at each side. The sternum, in contrast, is not only longer than any other but is prolonged backward as two egg guides, the hypovalves, or ventral valves, of the ovipositor (Fig. 7). There is a deep cleft at each side between the sternum proper and the hypovalves, and in this region the connection is membranous, allowing vertical movement of the valves. Numerous long, stout, yellowish setae are deeply set into the thickened, sclerotized apical and infolded dorsal margins (Fig. 23). These appear to be immovable or only slightly movable setae and are presumed to be instrumental in the placement of eggs.

In the membrane between the eighth and ninth terga, at about the level of the lower edge of the ninth tergum on each side, there is a small, sclerotized spot about the size of a spiracle. These small sclerites are most prominent in species of the *alexandriana* group. They are larger and more elongate dorso-ventrally in *albertensis* and *scita* but inconspicuous in these species be-



Figs. 19-22, *Chionea alexandriana*, 23, *Chionea nivicola*, details of female reproductive system. 19, internal reproductive organs, dorsal aspect: acg—accessory gland, bc—bursa copulatrix, egg—egg or ovum, fspth—functional spermatheca (anterior end of bursa), lovd—lateral oviduct (some ovarioles cut away, their points of attachment indicated by elongate ovals on drawing), spd—spermathecal duct, spth—spermatheca (inner lines represent outlines of masses of sperm), s9—ninth abdominal sternum, tc—trophocyte. 20, composite longitudinal section to show musculature of ovipositor; numbers indicate muscles (see text for origins, insertions and actions of numbered muscles; note ventral end of m-52 cut away to reveal cross-section of m-54). 21, bases of ducts of accessory glands enclosed in common covering. 22, sagittal section of posterior ends of bursa copulatrix and oviduct; abc—aperture of bursa copulatrix, covd—common or median oviduct, gfr—genital furca, gl—gland (cf. Fig. 44), gp—gonopore, mfb—muscles of furcal base, oacg—opening of accessory glands, pch—pouch between genital furca and upper wall of oviduct, spd—spermathecal duct, s9—ninth sternum. 23, hypovalves of eighth abdominal sternum, dorsal aspect; gp—gonopore.

cause of their pale yellowish color, and they appear to be absent in species of the *valga* group. I have not determined their significance.

Segments behind the eighth are reduced in diameter, their terga occurring above the elongate eighth sternum and their sterna partially or completely concealed. The ninth tergum is broadly fused dorsally with the tenth, from which it is separated laterally by a deep, narrow incision, below which the lateral extensions turn backward and inward to join the ninth sternum. The connection to the ninth sternum looks tenuous but is tough and not easily severed with dissecting needles. As used here the term ninth sternum means the sclerotized portion that is more darkly colored than surrounding membranous areas and is not cleared by potassium hydroxide in specimens prepared for mounting on microscope slides. Of course, this may not constitute the entire morphological ninth sternum, the limits of which have not been determined. This sclerotized portion may comprise simply two convergent bands, but more often a median plate, of variable shape depending on the species, is formed.

Between the ninth sternum and the upper surface of the eighth is the genital chamber into which the separate divisions of the reproductive system open (Fig. 22). Embedded in the membranous wall of the chamber just beneath the ninth sternum is the genital furca (see Byers, 1961*b*: 693), the arms of which join the ninth sternum and the base of which is attached to the roof of the common oviduct. Situated medially below the ninth sternum and bracketed by the arms of the furca is the aperture of the bursa copulatrix. The median or common oviduct rises sharply from the floor of the eighth sternum so that the gonopore lies not far below the opening to the bursa (Fig. 22). A deep pouch is formed between the furca and the lightly sclerotized upper wall of the oviduct.

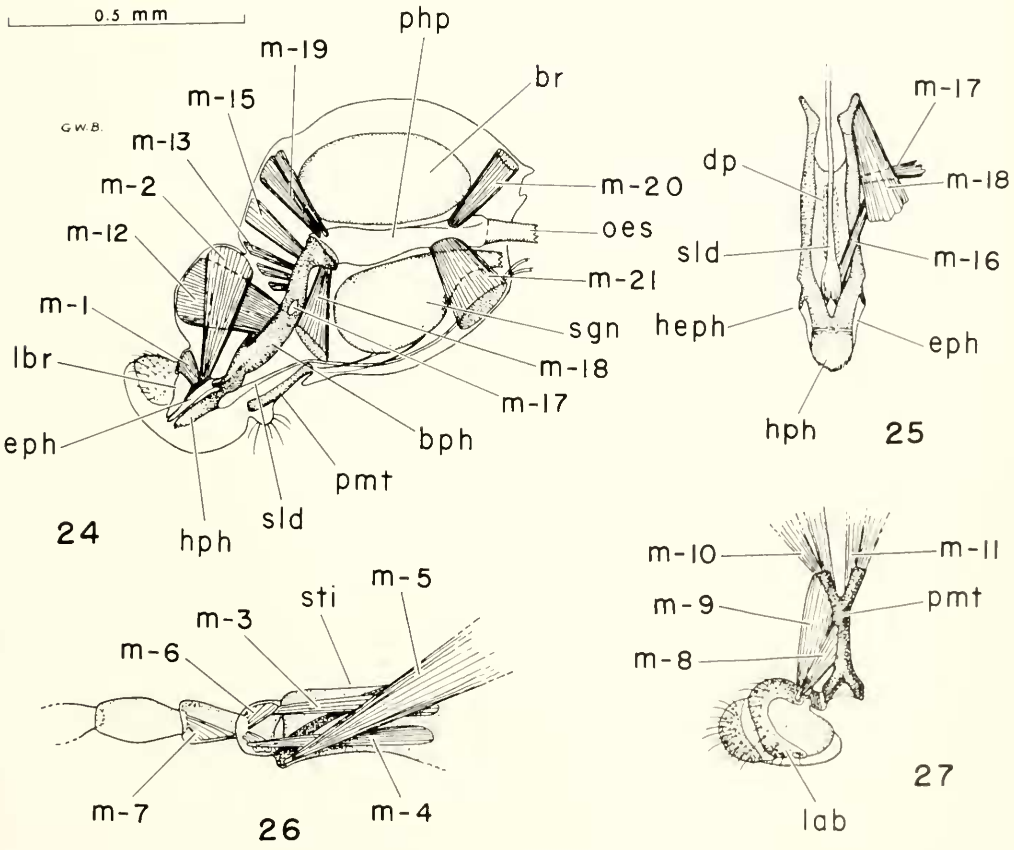
Less modified than the ninth, the tenth or pygidial segment consists of a well sclerotized, saddle-like tergum and a weakly sclerotized, sparsely hairy sternum, above which is the anal opening. Flexibly joined to the posterior end of the tenth tergum, supposedly arising between the tenth and eleventh, are the cerci (Fig. 7) which typically are elongate, sabre-shaped and strongly sclerotized, being especially thickened along their dorsal edges. A trace of sclerotization between the cercal bases may represent the eleventh segment. The cerci are often referred to as the dorsal or upper valves of the ovipositor. Scattered over their outer surfaces but particularly concentrated at the tips are a number of microscopic pegs set in circular bases. Although their histology has not been examined, these are presumed to be sensilla related to the detection of appropriate sites for oviposition.

ADULTS—INTERNAL MORPHOLOGY

Head.—Within the head, the most conspicuous structure is a large, compact mass of nervous tissue made up of the brain and suboesophageal ganglion (Figs. 24, 30). Seen from above (Fig. 29), the brain is clearly divided into right and left lobes, which appear to belong to the protocerebrum. These are curved downward at the sides (Fig. 30), concealing the poorly defined deutocerebral lobes from which the antennal nerves extend directly into the bases of the antennae. The optic lobes (Fig. 29) are remarkably small in relation to the large protocerebrum, probably due to the reduced number of ommatidia in the compound eye and hence fewer entering nerve fibers. Only a slight constriction at each side between the brain and the large suboesophageal ganglion indicates the position of the circumoesophageal connectives, and the ganglion and brain together make up an essentially continuous, broad, thick ring through which the pharynx passes (Fig. 30). From the lower surface of the suboesophageal ganglion, nerves were traced to the maxillary palps and to the labella. No nerves other than these and the antennal nerves were examined in any detail.

The pumping apparatus of the anterior digestive tube, together with its musculature, occupies most of the remaining space within the head. From the hypopharynx the digestive tube proceeds upward in the form of the rigid basipharynx, the sides of which are strongly sclerotized (Fig. 24). This joins the less strongly sclerotized pharyngeal pump, which is roughly triangular in cross-section (Fig. 30), concealed for most of its length by the brain and suboesophageal ganglion, and enlarged at the ends, where the muscles that operate it attach. From a membranous pouch at the junction of basipharynx and hypopharynx, where it enters the preoral cavity, the common salivary duct extends back along the ventral side of the head capsule, dividing just before the neck, one branch passing up along each side of the nerve cord as it comes off the suboesophageal ganglion (Fig. 24).

For ease of reference from text to figures, I have numbered the major muscles



Figs. 24-27, *Chionea alexandriana,* details of head and mouthparts. 24, internal structures of head, parasagittal section; bph—basipharynx, br—brain, eph—epipharynx, hph—hypopharynx, lbr—labrum, m—muscle (see text for origins, insertions and actions of numbered muscles), oes—oesophagus, php—pharyngeal pump, pmt—prementum, sgn—suboesophageal ganglion, sld—salivary duct. 25, basipharynx and hypopharynx, ventral aspect; dp—dorsal plate in membranous wall, for attachment of muscle 12, eph—epipharynx, heph—hinge of epipharynx, hph—hypopharnyx, m—muscle, sld—salivary duct. 26, maxilla and basal segments of maxillary palp, anterior (inner) aspect; m—muscle, sti—stipes. 27, labium, in part, anterior aspect; lab—labial palp (labellar lobe), m—muscle, pmt—prementum (prementum and mentum?). Scale: Fig. 24.

found in the head capsule and mouthparts and have listed them below by number, giving for each the origin, insertion and presumed action. Each numbered muscle or group of muscles is paired except where otherwise indicated.

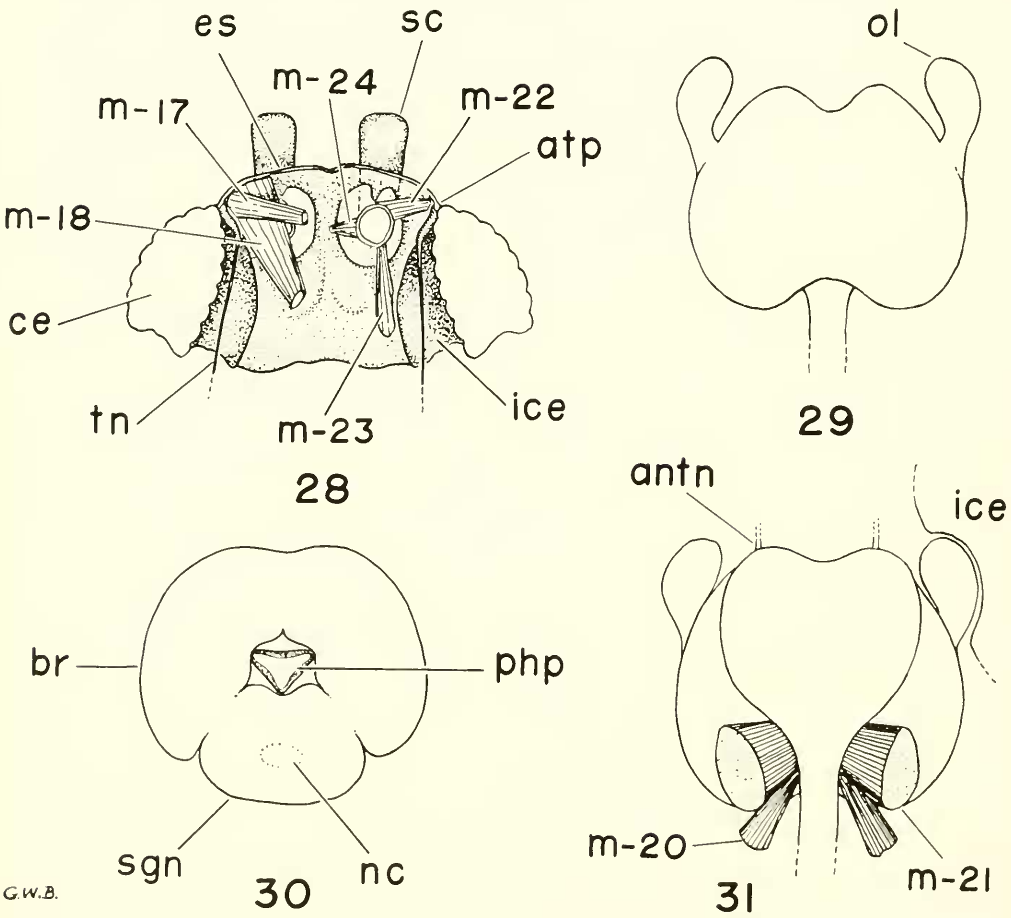
1. labrum to oblong sclerotized plate in the thin, almost transparent epipharynx; elevates epipharynx, distending cibarium (Fig. 24).

2. posterior clypeus alongside midline to end of oblong sclerotized plate of epipharynx; elevates epipharynx and draws it backward.

3-4. stipes (or sclerite in which it is embedded) to first segment of maxillary palp; respectively elevate and depress palp (Fig. 26).

5. head capsule below eye to distal end of stipes; adducts palp. (Abduction may be brought about by resilience of the stipes and associated sclerite.)

6. dorsal and ventral inner surfaces of first palpal segment to proximal rim



Figs. 28-31, *Chionea alexandriana*, details of head and anterior central nervous system. 28, internal (postero-ventral) aspect of frons; atp—anterior tentorial pit, ce—compound eye, es—epistomal suture, ice—inner surface of compound eye, m—muscle (see text for origins, insertions and actions of numbered muscles), sc—scape, tn—tentorium. 29, brain and anterior nerve cord, dorsal aspect; ol—optic lobe of brain. 30, brain (br) and suboesophageal ganglion (sgn), posterior aspect; nc—position of attachment of nerve cord, php—pharyngeal pump, in cross-section. 31, suboesophageal ganglion and brain, ventral aspect; antn—antennal or antennary nerve; ice—inner surface of compound eye, m—muscle.

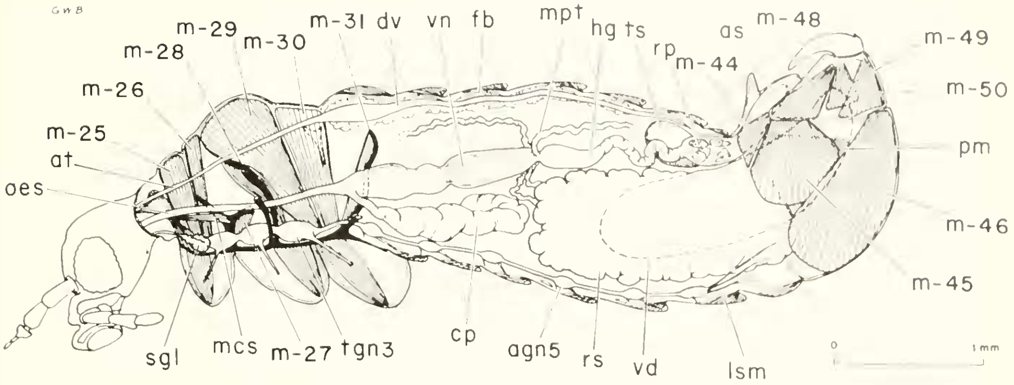


Fig. 32, *Chionea alexandriana,* internal structures of thorax and abdomen of adult male, composite of parasagittal sections; agn5—abdominal ganglion of fifth segment, as—anal (tenth) segment, at—aorta, cp—crop, dv—dorsal vessel (heart), fb—fat body (portion along dorsal vessel), hg—hind gut, or intestine, lsm—longitudinal sternal muscle, m—muscle (see text for origins, insertions and actions of numbered muscles; m-28 originates on mesothoracic furca; m-31 originates on metathoracic furca), mpt—malpighian tubule, oes—oesophagus, pm—pleural muscle from ninth sternum to ninth tergum (largely concealed by m-45; its outline indicated by dotted line), rp—rectal papilla, rs—reproductive system (enclosed in irregular portions of fat body; see vd), sgl—salivary gland, tgn3—thoracic ganglion of metathorax (fused with first abdominal ganglion), ts—testis, vd—vas deferens (position indicated by dashed line), vn—ventriculus.

of second segment; elevate and depress second segment.

7. side of second palpal segment to proximal rim of third segment; elevates third segment; no antagonistic muscle found.

8. mid-length of prementum to anterobasal surfaces of first segment of labellum; elevates labellum (labial palp) and rotates it on its basal attachment (Fig. 27).

9. proximal arm of prementum to posterobasal surface of first labellar segment; elevates labellum.

10-11. head capsule below and behind eyes to apex of proximal arm of prementum; elevates entire labium, drawing it into the head capsule.

12. anterior clypeus to elongate, sclerotized plate in semi-membranous dorsal wall of basipharynx; dilates basipharynx (Fig. 24).

13-14. head capsule along epistomal suture to dorsolateral edge of basipharynx (14: a pair of closely associated, small muscles); elevate proximal end of basipharynx.

15. frons near mid-line to semi-membranous roof of basipharynx; dilates basipharynx.

16. edge of head capsule near base of rostrum to basipharynx just above attachment of salivary duct; retracts basipharynx (Fig. 25).

17. edge of head capsule near anterior tentorial pit to side of basipharynx; moves basipharynx laterally, probably for maintenance of position and not for dilation (Figs. 24, 25, 28).

18. edge of head capsule below and in front of eye to proximal end of basipharynx; extends basipharynx (Fig. 25).

19. anterolateral vertex to anterior end of pharyngeal pump (two closely adjacent muscles); elevate end of pump and probably dilate it (Fig. 24).

20. lateral occipital region to posterodorsal surface of pharyngeal pump; a major dilator of pharyngeal pump (Figs. 24, 31).

21. posterior genal area to posteroventral surface of pharyngeal pump; a major dilator of pharyngeal pump (Figs. 24, 31).

The tentorium comprises two widely separated portions, very simple in structure (Fig. 28, tn), each a little thickened and irregularly bent anteriorly (probably the tentorial pit), then straight, extremely thin and thread-like to the posterior pit. There appear to be no muscle attachments along most of the length of the tentorium, but two small muscles (one to the scape and one to the basipharynx) originate on or very near the anteriormost end.

Three small, inconspicuously placed muscles (Fig. 28) move the antenna, all lying rather flat against the surface of the head capsule. Their origins, insertions and actions are as follows:

22. edge of head capsule, apparently on anteriormost tentorium, to anterolateral base of scape; moves antenna downward and sideward.

23. frons alongside inner margin of eye to posterior (upper) basal rim of scape; elevates antenna.

24. thin median bridge of frons between antennal sockets to mesal base of scape; adducts antenna.

Within the antenna the only muscles are those of the pedicel, originating respectively on the upper and lower surfaces of the scape, inserting on the basal rim of the pedicel and acting as elevator and depressor of the antenna.

The cervical sclerite has two small muscles inserted on its posteroventral edge, one from the anterior prosternum and the second from near the branch of the prosternal apophysis (Fig. 32, mcs).

Thorax.—It is hardly surprising that the indirect flight muscles, so conspicuous in the thorax of most Tipulidae, are not found in *Chionea*. The resulting space, however, both volume and surface for muscle attachment, has been largely taken up by the increased development of the muscles of the legs. To discuss the musculature it is first necessary to describe briefly the internal skeletal structure. This consists of three pairs of elongate sternal apophyses and the corresponding pairs of smaller pleural apophyses, as well as a low, median ventral keel running through all three segments. The prothoracic sternal apophyses (Figs. 13, 32) are widely separated basally. Each has an anterior arm, extending upward and a little outward to fuse with the very small pleural apophysis a short distance above the coxal process, and a slightly shorter posterior arm, which extends backward into the mesothorax. The mesosternal apophyses (Figs. 14, 32, as origin of m-28) are joined at the base, arising from the mid-ventral keel; they are unbranched, each with a flattened tip that has a muscular attachment to the blade-like, downwardly hooked pleural apophysis just below the vestigial wing. The metasternal apophyses (Fig. 15) are likewise joined basally, diverging abruptly and bent backward into the first abdominal segment (Fig. 32), the apophyseal arm having no connection to the pleural apophysis. Matsuda (1970: 319) noted that wide separation of the coxae does not greatly alter the exoskeletal structure from that seen in other Tipulidae.

Only the major muscles were examined in any detail. Again, these are numbered to facilitate reference from text to the illustration (Fig. 32).

25-26. pronotum and anterior mesonotum to ventral basal rim of trochanter of front leg; depress front trochanter, probably also femur.

27. posterior branch of prosternal apophysis to posterior edge of coxal base; remotor of front coxa. Note: promotor originates on mid-ventral keel and inserts on lower anterior edge of coxal base.

28. mesopleural apophysis and upper mesosternal apophysis to ventral basal rim of trochanter of middle leg; apparently one muscle from either side of the joined apophyses, both depressors

of the trochanter and probably also of the femur. Note: promotor of middle coxa originates on mid-ventral keel, its remotor on lower part of mesosternal apophysis.

29-30. posterolateral mesonotum and metanotum to ventral basal rim of trochanter of hind leg; depress hind trochanter, probably also femur.

31. apical half of metasternal apophysis to lower posterior edge of hind coxa; remotor of coxa. Note: promotor originates on mid-ventral keel.

A few of the lesser muscles deserve some comment. For example, there is a thin strand from the metapleural apophysis to the anterodorsal rim of the hind coxa. At the base of the haltere, seen from within (Fig. 35), there is a small, fan-shaped muscle serving to depress the haltere, which seems to be elevated by the resilience of the attachment. The wing vestiges appear to have no muscles at all.

Since the musculature of all legs is essentially the same, that of the hind leg will serve as an example. Figure 34 indicates the articulation and musculature of the right hind leg, seen from behind. The coxa is vertically hinged, the trochanter horizontally. Although the femur is scarcely movable on the trochanter, it does have a hinge-line from the anteroventral to posterodorsal rim of the recess in the trochanter (Fig. 37). Both the femoro-tibial and tibio-tarsal joints are dicondylic and horizontal, or nearly so, but thereafter the joints within the tarsus are monocondylic and not affected by direct muscles. Figure 34 shows the large depressors of the trochanter (m-29, m-30) entering from the thoracic cavity, passing through the coxa, and inserted on a long, paddle-shaped tendon attached to the ventral edge of the trochanter. The coxal remotor (m-31) has also been described earlier. Other muscles of the hind leg are (Fig. 34):

32. mid-ventral keel of metathorax to anteroventral edge of coxal base; promotor of coxa.

33. dorsal surface of coxa to spatulate tendon attached to anterodorsal edge of base of trochanter; elevates trochanter.

34. posterodorsal surface of coxa to small, disk-shaped tendon just above posterior condyle of trochanter; elevates trochanter.

35. posteroventral surface of coxa to ventral rim of base of trochanter; depresses trochanter.

36. anteroventral surface of coxa to

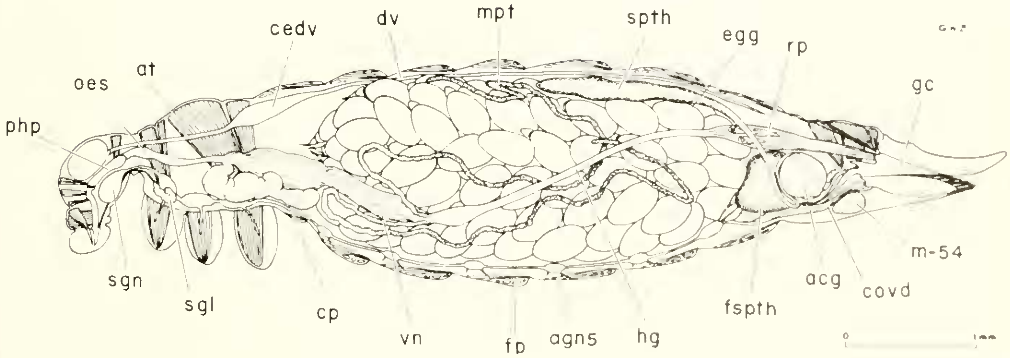


Fig. 33, *Chionea alexandriana*, internal structures of adult female, composite of parasagittal sections; acg—accessory gland, at—aorta, cedv—cardiac enlargement of dorsal vessel, covd—common or median oviduct, cp—crop, dv—dorsal vessel, fp—fat pad, fspth—functional spermatheca (anterior end of bursa copulatrix), gc—genital chamber, agn5—abdominal ganglion of fifth segment, hg—hind gut or intestine, mpt—malpighian tubule, m-54—transverse muscle of eighth sternum, oes—oesophagus, php—pharyngeal pump, rp—rectal papilla, sgl—salivary gland, sgn—suboesophageal ganglion, spth—spermatheca, vn—ventriculus.

ventral base of trochanter; depresses trochanter.

37. posterodorsal, posterior and posteroventral surfaces of trochanter to posterior base of femur just beyond hinge-line; moves femur slightly backward, very slightly upward.

38. dorsal surface of trochanter near base to posterodorsal base of femur just beyond hinge-line; moves femur very slightly backward and upward. Note: Snodgrass (1935: 197) says that when the femur is movable on the trochanter the action is production-reduction of the femur although only a reductor muscle is present. This muscle (m-38) appears separate, but it could be regarded as essentially continuous with the larger femoral muscle (m-37).

39. ventral and posterior surfaces of femur for nearly the entire length via a long tendon to ventral side of tibia near its proximal end; depresses tibia.

40. dorsal and anterior surfaces of femur in distal two-thirds or more via a long tendon to proximal head of tibia; elevates tibia.

41. dorsal surface of tibia, proximally, around posterior to ventral surface, distally, via long tendon to ventral base of basitarsus; groups of fibers spaced apart in distal portion of muscle; depresses tarsus.

42. dorsal and anterodorsal surfaces of distal half of tibia via long tendon to dorsal base of basitarsus; structure as in tarsal depressor (m-41); elevates tarsus.

43. ventral surface of tibia near proximal end to long unguitractor apodeme, which runs from unguitractor plate of pretarsus through tarsus, tibia and most of femur; retractor of pretarsal claws. This long apodeme has other, smaller muscles, but these were not observed in detail.

Origin in the mesothorax of large depressors of the prothoracic and metathoracic trochanters (m-26, m-29 in Figs. 32, 34) is unusual and needs some explanation. While the depressors of the hind trochanter in most insects originate in the metathorax, there has been such an increase in size in the posterior metathoracic muscle (m-30) in *Chionea* (and particularly in males) that the anterior group of fibers has been displaced forward into the space left vacant by the loss of the mesothoracic indirect flight muscles. Similarly, depressor m-25 has such an extensive origin on the pronotum that the posterior depressor of the prothoracic trochanter is displaced onto the anterior mesonotum, before the pseudosutural depression. This explanation, of course, avoids the question of why the depressors of the mesothoracic trochanter (m-28) do not originate on the mesonotum but on apophyses instead. A possible answer to this—or more specifically to why the muscles of the fore and hind trochanters should be so large as to crowd into the mesothorax—may be found in the insects' behavior. But to begin with it should be pointed out that the femoral muscles (i.e., those within the trochanter) are very small and that the joint between the trochanter and femur allows only slight movement. It may therefore be reasonably supposed that these large muscles not only depress the trochanter but serve as the primary movers of the femur as well. Accordingly, they and their counterparts in the mesothorax largely support the body during walking and are also used in a peculiar raising and lowering of the body when the insect is in a resting position (Fig. 50). In mating, the male often assumes a stance (Fig. 49) that throws nearly all his weight onto the hind legs and still requires a certain amount of locomotion. This may account for the greater development of the depressor muscles of the hind trochanter in males.

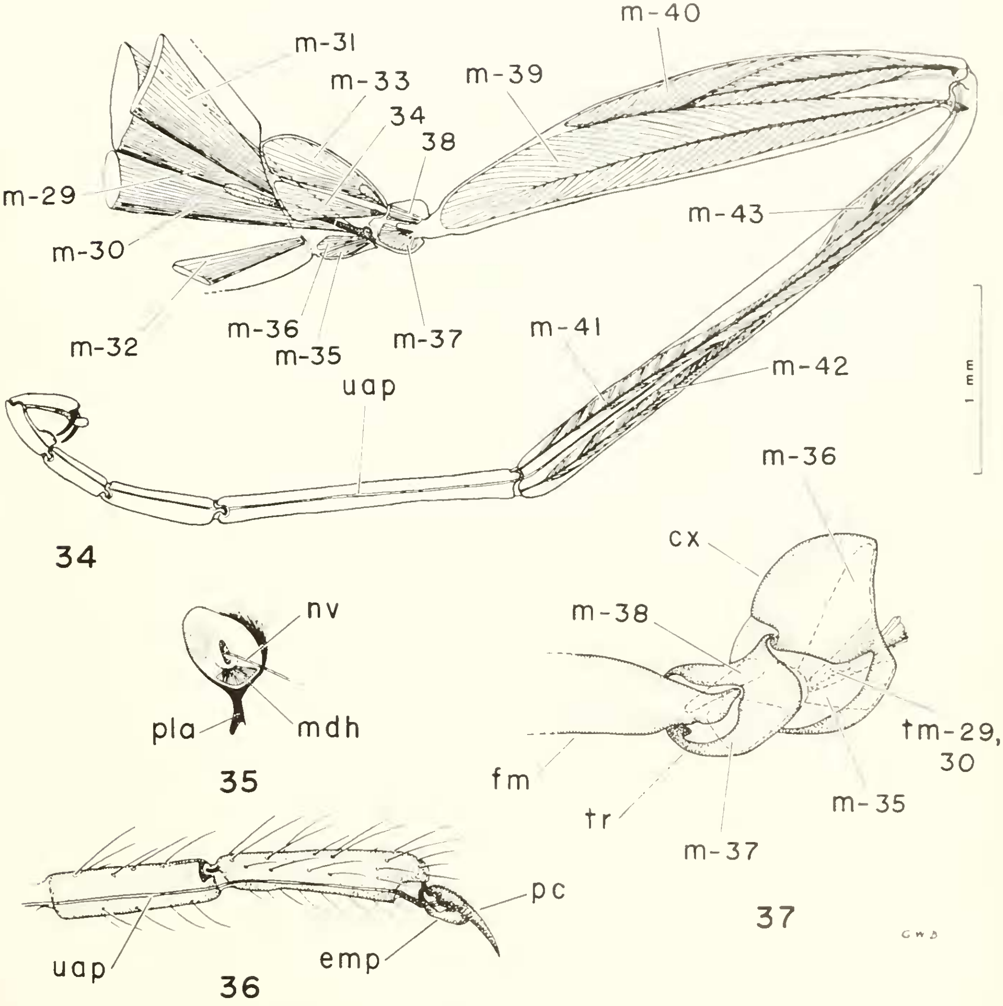
Need for support in walking would

also explain the large depressors of the tibia and tarsus. Most of the levator muscles, in contrast, probably are not often under much tension and hence are small. The levator of the hind tibia (Fig. 34, m-40), however, is relatively large, which explains the insect's ability to leap, an activity occasionally observed.

For the sake of continuity of description, the thoracic portions of the nervous, digestive, circulatory and respiratory systems will be dealt with below under the heading Abdomen.

Abdomen.—Contained within the abdomen are the entire reproductive system, most of the alimentary tract and dorsal vessel, and the greater part of the length of the central nervous system.

The body wall in the pregenital segments is rather simply constructed. In the



Figs. 34, 35, 37, *Chionea alexandriana*. 36, *Chionea lyrata*, thoracic appendages. 34, musculature of right hind leg, male, posterior aspect; m—muscle (see text for origins, insertions and actions of numbered muscles), uap—unguitractor apodeme. 35, interior aspect of base of left haltere; mdh—muscle, depressor of haltere, nv—nerve to interior of haltere, pla—pleural apophysis. 36, apical two tarsomeres and pretarsus; emp—empodium, uap—unguitractor apodeme, pc—pretarsal claw or unguis. 37, base of left middle leg, male, ventral aspect; cx—coxa, fm—femur, m—muscle (positions indicated by dashed lines; see text for origins, insertions and actions of numbered muscles), tm—tendon of muscles 29, 30, tr—trochanter. Scale: Fig. 34 only.

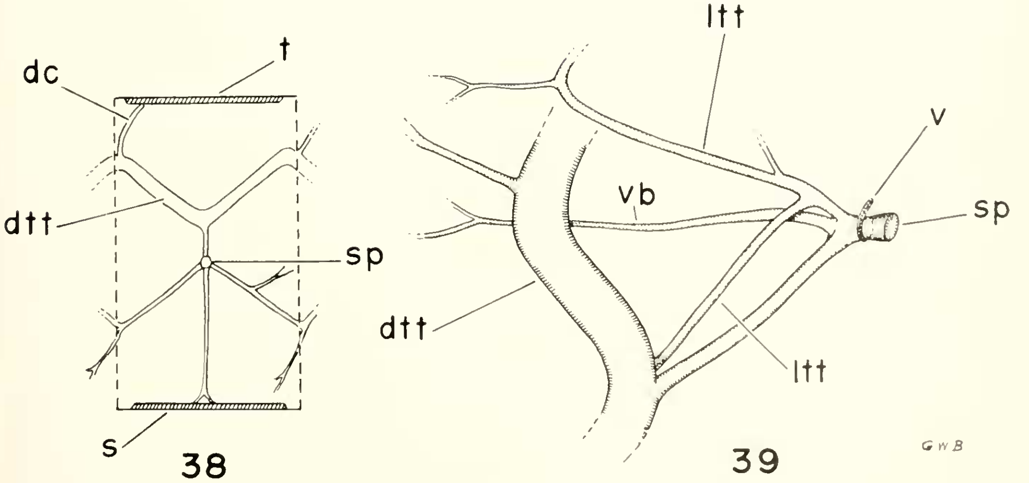
pleural region there are thin, flat, separated strands of muscle oriented vertically and attached to the small, oblong sclerites described earlier, which are assumed to be fragments of the terga and sterna. The sterna are linked by two sets of longitudinal muscle fibers: sparse and very thin inner strands extending from one antecosta to the next and shorter, more dense outer bands (Fig. 32, lsm) originating on the antecosta or nearby sternum and inserting on the next posterior transverse row of microsternites. These sclerites thus may represent the fragmented anterior margin of the acrosternite. Between terga the muscular connection is in general the same, but while the longitudinal ribbons of muscle lie side by side in a continuous sheet across the breadth of the sternum they are interrupted medially beneath the terga to make room for the heart, or dorsal vessel. Interspersed among the longitudinal muscle strands, wedged between them and the exoskeleton, and in general clustered against the body wall are numerous small, pad-like particles of fat tissue (Fig. 33, fp). These are most abundantly associated with the dorsal abdominal wall, and very few are found among the pleural muscles. In the female there is little other fat within the body except for a few short cords among the posterior reproductive organs. Males, however, usually contain large amounts of additional fat, both in the form of short, serpentine cords dispersed among all the abdominal viscera and as more extensive masses particularly in the anterodorsal part of the abdomen and along the dorsal vessel (Fig. 32, fb).

The dorsal vessel is thin-walled and (at least in specimens preserved in alcohol) flattened against the terga. Although the chambers in the heart or cardiac portion of the vessel are not well defined, there is a distinct widening of the vessel in the first two abdominal segments. From this cardiac enlargement the aorta extends more or less directly downward and forward to enter the head directly above the oesophagus.

From the suboesophageal ganglion the apparently undivided ventral nerve cord arches into the thorax to join the first thoracic ganglion, lying between the prosternal apophyses. The mesothoracic ganglion follows close behind the first and is separated from the metathoracic ganglion by a clearly double nerve cord, which is suspended in the fork of the mesosternal apophyses. Each thoracic ganglion gives off a pair of major nerves into the adjacent legs, as well as some lesser branches. There are six smaller, abdominal ganglia (agn), the first lying usually in the anterior second segment, the last in the seventh segment, and the others spaced approximately as shown in Figures 32 or 33. Each of the first five gives rise to a posterior pair of major nerves and an anterior pair of very slender nerves, all extending laterally and branching onto the body wall. From the back of the metathoracic ganglion, a pair of nerves resembling the larger ones from an abdominal ganglion arises medioventrally and extends into the first abdominal segment, suggesting fusion of the first abdominal and last thoracic ganglia. The terminal abdominal ganglion, which varies from two to three times as broad as the others, gives rise not only to slender anterior nerves but two pairs of larger nerves extending backward to the muscles of the genitalia, again suggesting the fusion of two or possibly three ganglia. In females (Fig. 33) the larger nerves from the last abdominal ganglion are of approximately equal diameter, but in males (Fig. 32) the first or outer pair are about twice the diameter of the second pair and lead into the basistyles. None of the nerves was traced beyond its basal portion. This description of the central nervous system is in fair agreement with that given by Brauer et al. (1854: Fig. 7) except in the structure of the brain and suboesophageal ganglion.

Extending backward through the thorax from the pharyngeal pump is the slender oesophagus, which joins the ventriculus, or mid-gut, near the anterior end of the abdomen (Fig. 32) or farther cephalad. Beneath the anterior end of the oesophagus, in the lower prothorax near the first thoracic ganglion, are the two irregularly shaped, nodular salivary glands (sgl). The ventriculus (vn) is thick-walled and muscular. It is usually somewhat constricted near its mid-length, but in various individuals other constrictions may also occur, the shape of the organ probably reflecting its physiological condition at the time of death and preservation. In a female whose abdomen is nearly filled with eggs, the ventriculus may be displaced forward and the hind-gut drawn more or less straight (Fig. 33). Just before the junction of the oesophagus and ventriculus, the crop joins the digestive tube ventrally. It is a large, membranous, rather amorphous organ, extending backward beneath the ventriculus, the posterior end often bent back cephalad. Although it is not easy to see how *Chionea* can take any food other than liquids, I have sometimes found rust-colored or greenish particles of solid material in the crop, as well as in the oesophagus. These may be precipitates, however, as they seem to have no cellular structure even at high magnifications.

Immediately behind the ventriculus, at the proctodeal valve, four Malpighian tubules (mpt) are given off, two dorsolaterally and two with their bases close together ventrally. In preserved specimens these have a faint purplish color throughout most of their length but are whitish in the basal one-fourth, which portion of the tubule is also more slender than the rest. They are subequal in length to the thorax and abdomen together and are usually intertwined among the viscera, although the apical portions may often be found lying atop the other organs, adjacent to the rectum or the dorsal vessel. The hind-gut (hg) is a fairly simple tube, enlarged only slightly at its anterior end but constricted just behind the attachments of the Malpighian tubules. Less thick-walled than the mid-gut, it may have a slightly annulated appearance due to the muscle arrangement. The rectum is situated dorsally, close beneath the seventh and suc-



Figs. 38, 39, *Chionea alexandriana*, details of tracheal system of adult. 38, diagram of major tracheae in typical abdominal segment, left side (anterior at right), interior aspect; dc—dorsal commissure, dtt—dorsal tracheal trunk, s—sternum, sp—spiracle, t—tergum. 39, detail of tracheae adjoining an abdominal spiracle (positional relationships distorted by mounting on microscope slide); dtt—dorsal tracheal trunk, ltt—lateral tracheal trunk, sp—spiracle, v—valve (sclerotized portion only), vb—ventral branch (to sternum).

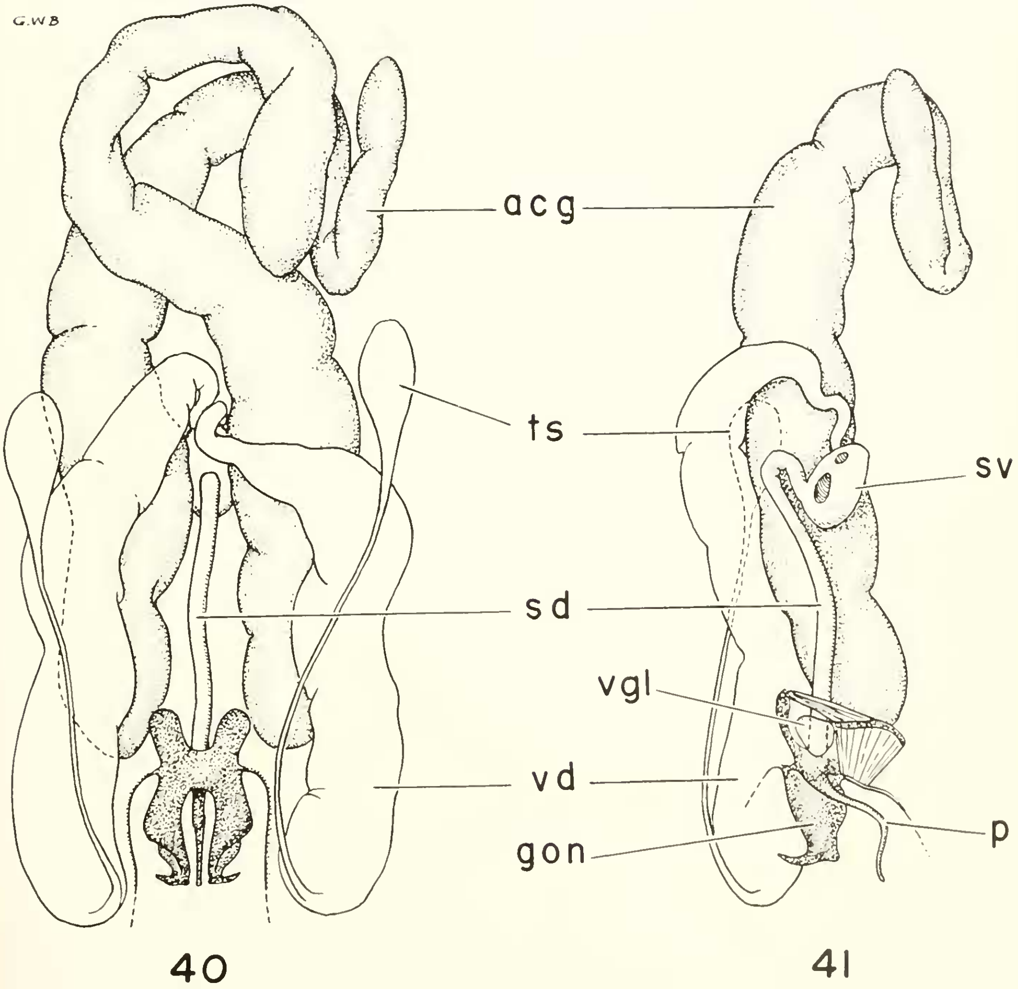
ceeding terga. It is membranous and semi-transparent, with four conical rectal papillae (rp) attached near the anterior end, their vertexes usually directed somewhat caudad. The number of these papillae has been reported as varying with sex in some nematocerous Diptera, but in *Chionea* it is four in both males and females.

I have not studied the tracheal system in detail, but the general pattern of it can be described (Figs. 38, 39). From the thoracic spiracles (sp) a large dorsal tracheal trunk (dtt) forms on each side and extends backward to the seventh segment, where it narrows abruptly and branches into small tracheae. Dorsolateral in general position within the abdomen and closely applied to the body wall, it bends downward above each abdominal spiracle to receive an incoming trachea from the spiracle, then rises again near the intersegmental line, thus forming a zig-zag pattern. The smaller lateral tracheal trunk connects the spiracles directly but bends downward between them, giving off a branch at the lowest point (Fig. 38). There is also a ventral branch trachea, so that in all there are four major branches entering from each abdominal spiracle (Fig. 39). These give off lesser tracheae, but the detailed pattern of branching varies even from one spiracle to the next in the same individual. Commissures (dc) connect the dorsal tracheal trunks in each segment. One trachea enters each leg, that of the front leg coming rather directly from the mesothoracic spiracle, that of the hind leg from the metathoracic, and that of the middle leg apparently formed by convergence of branches from both spiracles. In the tibia the tracheal diameter is as great as in the femur, but it diminishes in the tarsus. Two pairs of tracheae enter the head, supplying air to the anterior central nervous system and the feeding apparatus. Each of the abdominal spiracles opens into a short atrium, which is lined with hairs and which may be closed internally by a C-shaped sclerotized valve (Fig. 39).

Male Reproductive System.—Brauer examined the reproductive anatomy of *Chionea araneoides* more than a hundred years ago (Brauer et al., 1854: Figs. 8, 9), but in his illustrations he omitted the sclerotized structures and misidentified the softer parts. As far as I am aware, no one has since studied the internal structure of *Chionea*, so these errors have never been corrected. In another paper (Byers, 1961*b*: 696-700) I have described the reproductive system in a tipuline crane fly, *Dolichopeza*, and although this at first appears to differ extremely from the arrangement in *Chionea* there is actually a part-for-part correspondence, except for certain muscles. Accordingly I shall make occasional comparisons of the two genera in the following discussion.

Perhaps the internal reproductive structures in *Chionea* can best be understood by proceeding from the external genitalia already described. The genital chamber (Fig. 18) is the space between the basistyles, bordered above by the venter of the tenth segment (s10) and below by the ninth sternum (wgc). Its ventral wall or floor is membranous, but the anterior wall is strongly sclerotized, except at the edges adjoining the basistyles. The dorsal portion of this sclerotic region, from just beneath the tenth segment down to the base of the penis, is formed by the fusion of the bases of the gonapophyses. In *Chionea*, the vesica, a small sclerotized bulb from which the penis originates, lies at the surface and contributes to the anterior wall of the genital chamber. Extending downward and to the sides from the vesica are its two immovable lateral apodemes (la) (cf. Byers, 1961*b*: 699). Fusion of these apodemes along the mid-line is complete in some species of *Chionea*, such as *alexandriana*, but there may be a partial separation leaving a membranous area just below the base of the penis, as in *stoneana*.

On the lateral apodemes originate the thick muscles that activate the compressor apodeme (Fig. 18, cmca). In *Dolichopeza* I called this compressor apodeme of the vesica the dorsal apodeme (Byers, 1961*b*: 699), but in that genus the vesica and all its apodemes have rotated inward, maintaining their close association with the wall of the genital chamber only by way of a thin, membranous pouch that is an extension of the chamber. The mode of action of the compressor apodeme is discussed in the reference just cited. There is at either side of the median keel of this movable apodeme a broad extension, variously curved according to the species, which serves for the insertion of the compressing muscle on one side, and of the retracting muscles that expand the vesica on the other. The latter muscles originate on a second pair of relatively fixed apodemes that diverge cephalad from the vesica in *Chionea* (but are directed posteriorly in *Dolichopeza*, on account of the rotation



FIGS. 40, 41, *Chionea alexandriana*, reproductive system of male. 40, dorsal aspect. 41, right lateral aspect, organs of right side removed. Abbreviations: acg—accessory gland, gon—ponapophysis, p—penis, sd—seminal duct, sv—seminal vesicle, ts—testis, vgl—vesicular gland, vd—vas deferens.

described). These apodemes are connected by muscles (mg) to the adjacent ninth tergum and to the dorsal interior of the gonapophyses near their bases, and each receives a muscle originating at the side of the ninth tergum. The gonapophyses are only slightly movable.

Continuing inward from the vesica is the short, thick seminal duct (sd) (apparently the morphological ejaculatory duct), which leads to a small, thin-walled seminal vesicle (Fig. 41, sv), more or less median in position, in the seventh abdominal segment or thereabouts. At the sides of the vesica there are small, flattened pouches (vgl) connected around the anterior edge of the vesica to the seminal duct. While I could not find any evidence that these pouches are glandular in *Chionea*, their position suggests that they are homologous with the vesicular glands of *Dolichopeza*. There are two voluminous, dull whitish accessory glands (Figs. 40, 41, acgl), one lying at either side of the seminal vesicle and emptying into the vesicle by an extremely short tube behind the gland's midlength. From their points of attachment the accessory glands may extend posteriorly far into the ninth segment and anteriorly as far as the fourth or even the third abdominal segment. Their shape and size are extremely variable and probably fluctuate according to their physiological state and the volume of their contents. The glands may be elongate and thrown into one or two loops, or compartively short and thick, and the two in one individual are not apt to have even approximately the same shape (cf. Fig. 40). Their diameter also varies greatly, constrictions appearing here and there, so that the glands may seem to be divided into a number of compartments. No doubt this is what led Brauer to identify the anterior ends as the testes and the posterior ends as "paired appendages" of the seminal vesicle.

The vasa deferentia enter the seminal vesicle a little cephalad from the openings of the accessory glands. Although these tubes are quite slender where they join the vesicle (Fig. 41), they enlarge greatly in diameter as they curve upward over the accessory glands and remain distended for a major portion of their length. This enlarged part of the vas deferens (vd) is usually found packed with bundles of sperm, giving it a glistening, silky appearance, and probably is the functional seminal vesicle (cf. Snodgrass, 1935: 568) for, as mentioned earlier, that organ is very small. The thickened portion of the vas deferens ordinarily extends far into the ninth segment and often well into the basistyle. At its caudal extremity the vas deferens is abruptly narrowed, becoming a thread-like tube, which then reverses direction and passes back out of the ninth segment, terminating in a small, membranous sack, the testis. In his study Brauer overlooked the thin apical portions of the vasa deferentia and did not identify the sperm-laden enlargements. The relationship of parts of the male reproductive system is not easy to describe, but Figures 40 and 41 may make the above description somewhat more comprehensible.

Most of the muscles in the ninth segment are those of the genital appendages. On each side, however, there is a superficial sheet of muscle (Fig. 32, pm) connecting what might be termed the imaginary lateral margin of the ninth sternum with the equally imaginary lateral margin of the ninth tergum. Since the ninth segment is a continuous, well sclerotized ring, the function of these "pleural" muscles is not clear. Their action would be to draw the ninth tergum downward, somewhat flattening (depressing) the entire segment. The origins, insertions and actions of the other major muscles (Figs. 16, 32) are

44. anterolateral margin of ninth tergum to anterior base of basistyle; draws basistyle upward (forward).

45. anterolateral margin and pleural region of ninth segment to anterolateral base of basistyle; abducts basistyle and draws it forward.

46. ventral and lower lateral ninth segment (sternum) to posterior base of basistyle; draws basistyle downward (backward).

47. mesoventral ninth sternum to mesal margin of base of basistyle; adducts basistyle. Note: this is a large muscle, apparently responsible for the fact that preserved specimens of *Chionea* nearly always have the basistyles closed together, that is, drawn inward.

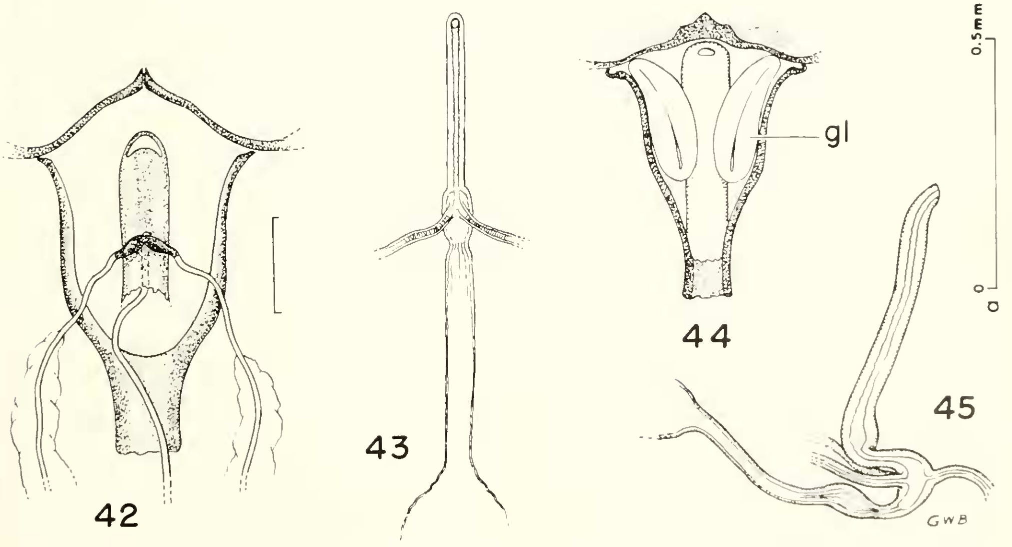
48-49. anterior and anteromesal basistyle to anterior base of dististyle; draw dististyle inward and forward, or "close" dististyles.

50. posterior basistyle to posterior base of dististyle; moves dististyle outward and backward, or "opens" dististyle.

In most respects the male reproductive system in *Chionea* is simpler than that in the Tipulinae, exemplified by *Dolichopeza*. Examples of its presumably less specialized design are the undivided dististyles, the simpler basistyles, which are not fused to the sternum, the non-rotated vesica, the straighter, shorter seminal duct and the wholly separate vasa deferentia (cf. Byers, 1961*b*: Figs. 17, 18, 27).

Female Reproductive System.—As in other crane flies I have studied, the reproductive system of females of *Chionea* consists of two separate parts: the bursa copulatrix and associated organs above, for reception and storage of sperm, and the ovaries and their ducts below. There is no internal connection between these two parts, but the external opening of each enters the poorly delimited genital chamber, as described earlier under external morphology, and to that extent they comprise a unified system.

The common or median oviduct is rather short, extending from the gonopore to just cephalad of the point where the



Figs. 42-45, comparative details of reproductive system of female. 42, *Chionea stoneana*, genital furca, ninth sternum, bursa copulatrix and spermathecal ducts, anterodorsal (interior) aspect (scale line 0.1 mm). 43, *Chionea lyrata*, bursa copulatrix and bases of spermathecal ducts, anterodorsal aspect. 44, *Chionea alexandriana*, genital furca, ninth sternum, bursa copulatrix and apparently glandular structures (gl) (cf. Fig. 22), anterodorsal (interior) aspect. 45, *Chionea nivicola*, bursa copulatrix and bases of spermathecal ducts, left lateral aspect. Scale a: Figs. 43-45.

base of the furca is anchored in the dorsal wall of the oviduct (Fig. 22, covd). Although thin-walled, it is muscular, having mostly transverse but also longitudinal muscles. The lateral oviducts (lovd) are extremely short as ducts alone, but each is continuous with the central lumen of its respective ovary, and the whole may be regarded as an elongate lateral oviduct giving off ovarioles in a radiating pattern along almost its entire length (Fig. 19). A female that has not commenced oviposition may contain as many as 200 eggs, the ovaries extending into the first abdominal segment and often even crowding into the thorax. A female of *Chionea nivicola*, for example, was found to contain 126 apparently mature eggs, of which eight were within the thorax (Fig. 48), extending even into the prothorax. The ovarioles are short, membranous and transparent, and each contains but a single egg. The older, more mature ovarioles are rounded apically, conforming more or less to the shape of the egg within, but toward the anterior end of the ovary most ovarioles contain in addition to the egg one or two smaller clusters of trophocytes, so that they are tapered at the apex (Fig. 19). In some other tipulids I have dissected, the distended ovaries had pushed the digestive tube aside, against the body wall. Perhaps it is sometimes so in *Chionea*, but in the females examined the digestive tube was found in the median plane, somewhat compressed between the ovaries, which being full of eggs bulged outward but were flattened medially.

Within the ovariole the egg lies with its anterior end (i.e., the end bearing the micropyle) away from the lumen of the ovary. The egg moves into the oviduct in this same position and thus is deposited posterior end first. Eggs in the dorsal part of the ovary are inclined downward, those in the ventral part upward, and so on, suggesting an inclined radial arrangement of the ovarioles around the lumen of the ovary (lateral oviduct). The eggs in both live females and those preserved in alcohol are whitish to very pale tan, those toward the anterior end of the ovary palest. They will be described later in more detail.

From its opening below the ninth sternum, the bursa copulatrix descends along the inner surface of the membrane between the branches of the furca (Figs. 22, 42, 44). It is only slightly curved cephalad near the base of the furca in some species (e.g., *Chionea alexandriana*, Fig. 22) but makes one complete loop in others (as *C. scita*, *C. nivicola*, Fig. 45). Approximately above the base of the furca there is a sclerotized thickening of the cuticular lining of the bursa, at which point the spermathecal ducts are given off. The lining of the bursa may be more extensively sclerotized and darkened, the degree depending upon both the species and the individual. In *C. valga*, for example, the bursa is very darkly sclerotized for most of its length.

Unexpectedly, the number of spermathecae was found to be either two or three. I would have expected a uniform number within the genus, but in females of *C. scita*, *C. nivicola* and *C. stoneana* there are three, while in *C. alexandriana* there are only two. The number of spermathecae could not be determined for every species because of a lack of properly preserved specimens in some cases; however, the bursa is ordinarily sufficiently sclerotized that it can be examined in cleared, slide-mounted specimens. It appears from such examination that the arrangement found in *alexandriana* (i.e., two spermathecae) occurs also in *lyrata* (Fig. 43), *nigra*, *excavata*, and other species of the *alexandriana* group. When there are only two spermathecae, the ducts open dorsolaterally on the bursa; when there are three, the third is medioventral in position. Also, when there are but two spermathecae, the ducts are large and thick-walled, while in species having three spermathecae they are thin-walled and slender. The ducts are either well sclerotized basally, as in *stoneana* (Fig. 42), or contain spiral, ctenidia-like reinforcements near the base, as in the *alexandriana* group (Fig. 43).

The spermathecae are not sclerotized and of fixed size as in some other crane flies, such as *Dolichopeza* (Byers, 1961*b*: 701), but have membranous or semi-membranous (i.e., somewhat thickened yet translucent) walls and vary in size according to species, as well as with the volume of sperm contained. The female illustrated in Figure 19, for example, had distended spermathecae which were packed with sperm, but in some other females of the same species the spermathecae were small and wrinkled. The position of the spermathecae is highly variable, and the ducts are usually irregularly curved or even looped.

From the point at which the spermathecal ducts enter, the bursa copulatrix continues cephalad, terminating in a pouch (Fig. 19, fspth) that, like the spermathecae, has membranous to semi-membranous walls. It is large in females of the *alexandriana* group (the actual extent determined only in *alexandriana* but inferred from the part visible in slide-mounted specimens of the other species) but small to minute in other species. This appears to be the morphological equivalent of the "functional spermatheca" of *Dolichopeza* (Byers, 1961*b*: 703). In *Chionea*, however, I have never found any sperm in this pouch, while the spermathecae may be filled with them, as in the specimen illustrated (Fig. 19). The walls of this pouch are finely rugose, with abundant hair-like filaments extending into the lumen. The contents in preserved specimens are sparse aggregations of minute particles. Since the concentration of spermatozoa in the spermathecae is as dense as that in the vasa deferentia of the male, leaving virtually no space for any fluid carrier such as is probably produced in the male's accessory glands, it may be that the fluid portion of the semen received is stored in the pouch at the end of the bursa. Whatever its function, it is in some species a structure of considerable capacity situated where it is likely to be involved in the reception and storage of some part of the seminal fluid.

There are two accessory glands which empty by slender ducts (sometimes enveloped in a common sheath, basally, as Fig. 21) into the bursa just inside the aperture. These vary in size and general appearance from one individual to the next, being sometimes turgid and conspicuous (Fig. 19), other times so small and wrinkled as to be easily overlooked. Such differences are probably indicative of the physiological state of the organs at the time of preservation, the glands possibly being distended shortly before oviposition and collapsed after a batch of eggs has been laid. Closely applied to the membrane between the furcal arms and lying one at either side of the bursa are a pair of elongate, subhyaline, seemingly hollow structures (Figs. 22, 44, gl) of unknown function. These are usually very difficult to see. They appear to have no attachment to the bursa but may open to the outside near the ends of the arms of the furca. I have designated them "glands" (gl) with doubt.

Nearly all the major muscles in the eighth through tenth abdominal segments of the female are concerned with the deposition of eggs. Since I have not observed oviposition in *Chionea* and consequently do not know how the valves of the ovipositor move, I can only speculate on the function of certain of these muscles. Thei origins, insertions and actions (see Figs 20, 33) are as follows:

51. dorsolateral region of eighth tergum to anterodorsal corner of eighth sternum; elevates anterior end of eighth sternum.

52. lateral ends of eighth tergum to side of eighth sternum, below margin and beside gonopore; elevates eighth

sternum. Note: it cannot be surely said which of the described attachments is the origin and which the insertion.

53. anterior eighth sternum to lateral portion of ninth sternum; draws ninth sternum downward. Note: muscle pairs 51-53 probably function to bring the gonopore and the opening of the bursa copulatrix into proximity so the eggs can be fertilized at the time they leave the oviduct.

54. side of eighth sternum to opposite side, passing just beneath and behind common oviduct; draws sides of sternum and therefore bases of hypovalves together. Note: this unpaired muscle together with pairs 51 and 52 may be involved in extrusion of the egg from the posterior end of the oviduct.

55. posterodorsal eighth sternum to anteroventral hypovalve; elevates hypovalve.

56. dorsal ninth tergum to base of cercus; depresses cercus (see also m-58).

57. dorsolateral ninth tergum to lateral ninth tergum near attachment of ninth sternum; elevates ninth sternum.

58. dorsal tenth tergum to base of cercus; depresses cercus (see also m-56).

59. transverse, infolded ridge on tenth tergum to upper base of cercus; elevates cercus. Note: the elevators of the cerci are very small, while the depressors are large, indicating that the cerci are probably drawn down against the hypovalves during oviposition.

60. lateral tenth tergum to lateral tenth sternum; elevates tenth sternum.

There are some lesser muscles associated with the furca, including those between the furcal base and the oviduct (Fig. 22, mfb). The membranous body wall at each side of the pouch (Fig. 22, pch) between the furca and the distal roof of the oviduct also contains a wide, thin sheet of muscle attached to the furca.

NATURAL HISTORY OF CHIONEA

Ecological Distribution

Although there is a slowly growing body of knowledge about the underground habitats of *Chionea*, the fact remains that most of what we know about these flies is based upon their occurrence on the surface of snow. Against the white background of snow even the palest *Chionea* is conspicuous, especially when moving. In contrast, the flies would be easily overlooked in the winter surface vegetation, which is largely dead and dried to dull browns and grays. On the surface of snow, species of *Chionea* may be found together with such other winter insects as *Boreus* spp. (Mecoptera: Boreidae), various apterous, brachypterous or even fully winged stone-flies (Plecoptera: Nemouridae, especially Capniinae), gall wasps (Hymenoptera: Cynipidae) of the agamic generation, several kinds of snow-fleas (Collembola: Poduridae and Isotomidae), certain Chironomidae, Anthomyiidae, and a few taxa of non-insect arthropods, notably spiders. By "found together," I mean they occur in the same general environment. Insects on the snow are usually widely dispersed, and I have never seen any direct interaction of a *Chionea* with any of the other kinds of arthropods mentioned.

Activity of winter insects on the snow seems to be limited mainly by temperature and to a somewhat lesser extent by wind and blowing snow. Light intensity may also be an important factor in the case of *Chionea*, as will be discussed later, but its effect is not readily separated from that of temperature.

While the relationship of such physical factors of winter environment to the distribution and abundance of various insects has been examined by several authors, few of these studies have direct bearing on the biology of *Chionea*. Cold hardiness in some European winter insects, including *Chionea araneoides* Dalman, was studied by Sömme and Östbye (1969). They found this *Chionea* active chiefly at air temperatures of 0 to −4°C, occasionally at −7°C (near 20°F). They determined that it is able to avoid the lethal effects of freezing of its haemolymph by supercooling to −7.5°C. From his field observations of *C. araneoides*, Hågvar (1971) determined −6°C to be the lower limit of activity and found the flies most commonly on the snow at air temperatures between −4 and −5°C when there was no appreciable wind. He seldom saw this species on the snow at even slightly higher temperatures (−3 to 0°C) and concluded that their activity is very narrowly limited by temperature. Wojtusiak (1950) found *Chionea* (*lutescens* and "*hrabei*") active primarily around −3.5°C. Bezzi (1919) reported *Chionea* spp. active at temperatures down to −6°C.

Chapman (1954) similarly found some North American Chioneas (mostly *C. alexandriana*) active on snow at air temperatures in the range of −7 to 0°C but mainly between −4 and 0°C. He also found *C. alexandriana* in cold stupor at −7.5°C (19.5°F). His observations are in close agreement with those of Sömme and Östbye.

Throughout the range of *Chionea*, winter temperatures far below this tolerable level of approximately −7°C are frequent and often of many days' duration. It is accordingly imperative that the flies have ready means of escape from severe cold. Routes for movement from the snow surface to the soil are easy to find when one is in the natural habitats of *Chionea*. They may result from accumulation of gently falling snow on low vegetation, often leaving adequately large openings to the soil. Others occur around large trees and rocks, where surface wind may arrange the snow in such a way as to leave large, funnel-like depressions leading to the soil or nearly so. Winds also move brush, saplings and other vegetation protruding above the snow surface from side to side, with the result that around the stems of such plants there are narrow channels leading down to the ground.

The insulating effect of snow cover on the soil cannot be overemphasized. Mail (1930: 579) showed that temperature just below the soil surface (habitat of larval Elateridae, or wireworms) fluctuated only about 4°C (−1 to 3°C) over a month of observations (January), while air temperature above the snow varied from −2 to −23°C around a mean of about −14°C. He also demonstrated (p. 577) the cooling effect of air temperature on the soil in the absence of snow cover. Coulianos and Johnels (1962) recorded similar results for the subnivean environment of small mammals. (The subnivean air space results when snow is held away from the soil surface by grasses and other low vegetation; it may be enlarged by the activities of mammals or perhaps by heat generated by bacterial decomposition of leaf litter or other dead vegetation.) These investigators found that over a 14-day period in March in Sweden, the temperature in a 5 cm subnivean stratum beneath 20 cm of snow varied only from 0 to 2°C, while during the same period daily maximum temperatures fluctuated between −6 and 0.5°C and nightly minima between −4 and −23.5°C. In another study of microclimates to which small mammals are subjected, Hayward (1965) found that in burrows of *Peromyscus* mice in alpine, subalpine, mesic and arid habitats, winter temperatures never fell below 0°C. (Although it is not particularly relevant here, Hayward further found that in summer, when air temperatures during a day might fluctuate 15.2 degrees, from 4.6 to 19.8°C, the temperature in representative mouse burrows remained very close to 10°C.)

I have made similar comparative measurements of temperature in the soil, in the snow cover, at the snow surface and in the air several centimeters above the snow surface. My findings, while only made on certain days and in various winters, not over a span of many days, agree with those presented here.

By seeking refuge in soil cavities, in rodent burrows, or in the subnivean air space, *Chionea* can not only escape severe cold at the snow surface but can in fact enjoy a habitat where the temperature is relatively stable, probably near the optimum for the adults, and where the humidity is relatively high. In view of these effects of snow cover, one wonders if *Chionea stoneana,* our least boreal species, might not be also our most cold-hardy *Chionea,* living as it does in a mid-continent region where winter temperatures are often very cold but where snow cover is frequently absent.

Where Chioneas are and what they are doing when they are not on the snow surface is only sketchily known. Chance observations by a number of authors have appeared chiefly in the European literature. Bezzi (1919) summarized 67 collections of *Chionea* made up to 1917 in Europe and Asia. He recorded six collections from caves (two from France, four from Jugoslavia), two from vacant underground wasp nests in Belgium and the Netherlands, and one from the burrow of a meadow vole (*Arvicola*). Bezzi did not regard *Chionea* as a cavernicolous insect but supposed that the flies had only accidently wandered into caves in search of smaller cavities in which to conceal themselves. There are sufficient records from caves in the United States, however, to convince me that *Chionea,* while perhaps not a cavernicole in the strict sense, is more than an accidental visitor in caves. There have been a few subsequent discoveries of *Chionea* in European caves (e.g., Strinati and Aellen, 1967).

In a study of cave insects, Dr. M. S. Briscoe of Howard Univ. set a number of pitfall traps (glass jars) in the floor of a cave near Harpers Ferry, West Virginia. These were baited with decomposing meat and were intended to attract primarily cave-dwelling Coleoptera. In addition to the beetles and various other insects, Dr. Briscoe trapped 29 specimens of *Chionea scita,* a larger collection of this species, by far, than any ever made from the snow surface. The traps in which *C. scita* was found, Dr. Briscoe informed me, were set 100 ft (31 m) or more inward beyond the border of total darkness in the cave.

During summer months crane flies are not uncommonly found in the entrances to caves, that is, in those parts of the cave that afford shade from the sun and increased humidity but are not isolated from the more normal environment of the flies; but such crane flies rarely venture into a cave beyond the zone of deep twilight. Graham (1966) has given an account of this, as well as of the occurrence of the trichocerid flies *Diazosma subsinuata* (Alexander) and *Trichocera columbiana* Alexander in the zone of total darkness. I have occasionally found large numbers of mosquitos and fungus gnats hibernating in parts of caves that were totally dark yet not a great distance from the opening. It is likely that some fungus gnats (Mycetophilidae) can breed in caves, where such organic debris as bat guano accumulates on the floor to provide adequate substrate for the growth of fungi which in turn nourish the larvae. While the diet of larvae of *Chionea scita* is not yet known, there is a strong likelihood that it is comprised in part of organic debris of various sorts. It is thus not improbable that the population sampled by Briscoe had become established in the cave.

Mr. Roger Sperka (pers. comm.), then of the Univ. of Kentucky, collected a female of *C. scita* in Wind Cave, Pulaski Co., Kentucky. He estimated that the fly was found 700 ft (215 m) from the entrance and in a lateral tunnel, thus far beyond the darkest crepuscular zone and in total darkness, where the temperature was 51.5°F (11°C). However, the single individual had fallen into a small stream in the cave, had clambered out again and "seemed disoriented," so there is reason to suppose it may have strayed from some area of the cave where a population of its species might have been established, if not from outside the cave.

Other records from caves involve primarily western species taken considerably closer to the cave entrances. The flies in these instances could have been accidental visitors. A collection of special interest is that of *Chionea alexandriana* from an ice cave in Union Co., Oregon. The single male in this collection of 18 individuals has gonapophyses of an atypical form not seen from elsewhere in the range of the species.

Underground habitats of *Chionea* other than caves consist almost wholly of burrows constructed by other kinds of animals. These vary in size from burrows of earthworms (Kryger, in Edwards, 1936) to nest burrows of wasps (Bezzi, 1919) (conceivably enlarged from rodent nests) to burrows and nests of mice and voles.

Hackman (1961, 1963*a*, 1963*b*) has made the most detailed and systematic study of Diptera in excavations made by small rodents. Among some 2000 individual flies of 240 species, he found only one *Chionea*, a female of *C. lutescens*. This fly was in a burrow of *Clethrionomys glareolus* beneath a tree stump in southern Finland. Hackman (1963*a*) regarded *C. lutescens* as a xenocoenic species, that is, one that is foreign to the community in which it has been found (in this instance the burrow community) and actually adapted to life in some other kind of habitat. Trichoceridae, or winter gnats, were common in his winter samples; he found four species of these (also two of the crane fly genus *Ormosia*, but not in winter). These he regarded as tychocoenic, generally adapted to the burrow environment but with a wider ecological range enabling them to thrive in other, similar biotopes as well. Hackman concluded that *Chionea* merely utilizes the vole burrow as a shelter against unfavorable weather in winter, although he pointed out that the deep burrows communicate with runways in the subnivean air space. In his interpretation of the presence of *Chionea* and *Trichocera* in burrows of *Clethrionomys*, he possibly overlooked one aspect of the biology of these flies, that is, larval diet. Larvae of *Trichocera* develop in decomposing organic debris such as may accumulate in rodents' excavations, particularly nests. There is also reason to believe that such nest debris (e.g., feces of mice) is involved in the diet of larvae of *Chionea*. That is, I am suggesting that *Trichocera* and *Chionea* may spend much of their respective life cycles in rodent burrows.

The extent to which rodent burrows or nests are utilized by North American species of *Chionea* is not known. We may make some inferences, however, from certain facts about *C. stoneana* and *C. scita*. Investigation of arthropods in nests of the prairie vole, *Microtus ochrogaster* Wagner, by Philip C. Stone of the Univ. of Illinois, led to the discovery of the specimens upon which Alexander (1940) based the description of *C. stoneana*.

Fourteen adult males and five females of *C. stoneana* were collected from cavities beneath large logs, apparently abandoned mouse nests (probably of *Peromyscus leucopus*), on 2 January, in a sparse oak-hickory woodland in northern Franklin Co., Kansas. The nest material upon which the adult flies were walking, and from which numerous larvae were subsequently recovered, consisted of finely shredded, decayed wood, small fragments of dead leaves and grass stems, and some loose soil particles. Arthropods associated with the Chioneas included small, active staphylinid beetles and some hibernating, inactive wood cockroaches, ants, lygaeid bugs and a machilid. Further details are found in the account of *C. stoneana* following.

A habitat in southern Michigan from

which I obtained several individuals of *C. scita* was in many ways similar to that just described. The flies were in cavities beneath two old, rotting stumps, where the accumulated material comprised shredded or crumbled decayed wood and bits of dead leaves and grasses. Both stumps were about 3 m from the marshy edge of a lake, about 50-60 cm above the water level.

It has been noticed from the time of Bezzi's 1919 monograph onward that *Chionea* species are found only in environments that are to some extent forested. It is furthermore clear that the particular kind of forest is not a factor in the ecological distribution of *Chionea* at the generic level, nor does it seem to be for any species. Trees, of course, may play a dual role in the environment of *Chionea*, shading the terrestrial habitat in summer to provide a more nearly uniform temperature the year around, and serving as windbreaks in winter when *Chionea* is on the snow surface.

In eastern North America *Chionea* occurs in deciduous woodlands, such as the relatively dry oak-hickory or the more moist, boreal-montane beech-maple associations, also in mixed deciduous and evergreen forests of eastern Canada. In the western mountains, *Chionea* may be found from the rather low and dry forests of ponderosa pine (western yellow pine), through the higher zone of lodgepole pine, and in the high alpine forests of spruce and fir. Within these various kinds of forests, *Chionea* often is found in clearings or areas of sparse timber and along streams, less often in dense stands of trees. In contrast, no species seems to occur on treeless plains or in mountains above timberline (although *C. nigra* has been collected up to 11,400 ft (3500 m) in the Rocky Mountains of central Colorado, which is just below timberline at that latitude). Wherever *Chionea* occurs, there will be found some vegetation penetrating through the snow cover. It should be borne in mind, though, that these insects are strong walkers and may wander an appreciable distance from such vegetation. A case in point is the discovery by E. N. Pruitt of *C. valga* on the ice of frozen Lake Huron, northern Michigan, 46 m (50 yards) from the shore.

A further observation concerning the general habitat of *Chionea* is that the terrain is nearly always rocky, that is, with protruding rocks here and there. This has not proved true for most habitats of *C. stoneana*, however. Sufficiently large rocks are likely to have the snow drifted around them in such a way as to give access from the soil to the snow surface. Durbin (1975: 139, Figs. 16, 17) illustrates this very well. It has occurred to me that, at least in the habitats of the lowland eastern species, this association of *Chionea* with rocky places may derive largely from the works of humans. That is, where the land is more or less level and not rocky, it has been cleared of trees and used for agriculture.

Geographical Distribution

North American species of *Chionea* fall into two main distributional groups, eastern and western, which have no relation to the taxonomic groups already discussed.

The eastern geographic group (*valga, scita, stoneana* and *wilsoni*) includes fairly widely ranging species that have so far been taken only at relatively low elevations. As a group these have spread out over a vast area more than 2000 miles from east to west and over 1500 miles (21 degrees of latitude) from north to south. An interesting aspect of this extensive distribution is that a major part of the ranges of three of these species falls within the area that was glaciated at various times during the Pleistocene and was overlain by ice as recently as about 10,000 years ago. Nearly the entire range of *C. valga*, the most widespread species in the genus, is in the formerly glaciated region. There is no reason to suppose that the range of *valga* was displaced very far to the south of the glacial border during the Wisconsin advance, but even so the flies must have walked some 1200 miles (or more, depending upon the range during the glacial maximum) to reach certain portions of the species' present range. This sounds impressive but actually amounts to somewhat more than 195 m (210 yards) per year, probably not an unusual distance for an individual *Chionea* in its lifetime. (I am not considering any more rapid means of dispersal than the insects' own movement.)

It is often the case that tipulids having such a boreal forest distribution as that of *C. valga* also occur southward through the Appalachian Mountains, but on the basis of available evidence this seems not to be generally true of *valga*. Although the southernmost part of its range is in the Appalachian region, the collection localities are not particularly montane. However, the southernmost record of *C. scita* in northern Georgia is decidedly montane, about 3200 ft (985 m) above sea level.

Even more a species of the flat-lands is *C. stoneana*, which possibly was isolated in the Ozark-Ouachita region during the Wisconsin glacial advance and which has, as far as we know, moved only 450 mi or so into formerly glaciated territory.

In contrast, the western geographic group is primarily montane in distribution. Only about the northern one-fourth of the group's range was covered by the continental ice sheet, but doubtlessly the rest of it was influenced by extensive mountain glaciers during the late Pleistocene. The combined ranges of the 12 western species (*albertensis*, *alexandriana*, *carolus*, *durbini*, *excavata*, *hybrida*, *jellisoni*, *lyrata*, *macnabeana*, *nigra*, *nivicola* and *obtusa*) cover an area about 1,600 mi from north to south and about 1,300 mi from east to west. Within this area, however, the ranges of the various species of *Chionea* apparently follow the mountain chains, leaving broad "vacant" areas, such as in the northern Great Basin.

Collection of the snow-inhabiting mecopteran, *Boreus*, in such far northern localities as the Pribilof Islands and central Alaska invites speculation about whether *Chionea* might not also occur there. Representatives of the two genera are often found together on snow in both eastern and western North America, suggesting they have a number of ecological requirements in common. Both genera are flightless, *Boreus* therefore having no obvious advantage in distribution. Observations of *Chionea nigra* and *Boreus coloradensis* in the Rocky Mountains of central Colorado indicate that *Chionea* is even more tolerant of low temperatures than is *Boreus*. It seems unlikely, however, that *Chionea* will be found in the Arctic or in subarctic areas north of approximately 60°, except where proximity to the ocean has a moderating effect on temperature. The winters in this region are probably too harsh—the temperatures persistently too low.

These distributional data emphasize that the ranges of the western species in particular, but of the eastern ones as well, are still only sketchily known.

Seasonal Distribution

It is not practicable to attempt to summarize the seasonal occurrence of *Chionea* in North America except in the most general way. Data on seasonal distribution are given in detail and briefly summarized for each species in the taxonomic accounts which follow. There are collection records of one species or another for every month from September through May, with peaks of abundance of adults coming generally in October-November and February-March.

Variables in seasonal distribution of any species include latitude and elevation of the collection site and the weather of the particular year. Latitude is of greatest importance in such a species as *Chionea valga*, the range of which spans more than 15 degrees of latitude but includes little altitudinal variation. Elevation, of course, influences the season of appearance of adults mainly in the western montane species. Since weather can vary so greatly from one year to another, the data on seasonal occurrence based on occasional chance collections are not very meaningful. Detailed studies in certain areas over an entire winter are more significant. Chapman (1954), for example, found peaks for *Chionea alexandriana* in western Montana, between 3600 and 7000 ft, in November-December and February-early April (but the species was still present on the snow in mid-May). Somewhat further south but at higher elevations, 9500-11,200 ft in the Rocky Mountains of Colorado, Osburn (1958) found *C. nigra* most abundant in October-November and late February-April. In the Sierra Nevada, at 6200 ft, Durbin (1975) found adults of *C. carolus* from early November to early February, with a clear peak of abundance in December.

Longevity of Adults

Most summer crane flies have a rather ephemeral existence as adults—generally a few days, some surviving for perhaps a week or ten days under most favorable conditions. In contrast, species of *Chionea* are relatively long-lived, the supposition being that cold winter temperatures slow their physiological processes and proportionately increase longevity. It is not yet possible to state the duration of adult life of any species of *Chionea* because no individual fly has ever been observed from its emergence from the pupa to natural termination of life. The longest I have kept adults was 19 days after they were collected. Edwards (1936: 89) recorded survival of *Chionea lutescens* for 62 days, including a trip by air-mail from Denmark to London. I anticipate that adult longevity of two months will be found not uncommon in North American species though it will not be easy to determine. Removal of the insects from their natural surroundings may spare them from predation or severe weather, but I suppose any laboratory environment has its own perils that may not be evident to the entomologist.

Long adult life could be viewed not only as a physiological response to cold but also as an adaptation to fluctuations in weather. There are likely to be periods of many days and nights together when the air temperature remains below the level at which *Chionea* can survive. Accordingly, activities that normally take place on the snow (or other) surface have to be postponed. A prolonged period of adult emergence (from the pupal stage) would of course also help to overcome this environmental obstacle, but so far we have no data that would separate this from individual longevity.

Behavior

What follows concerning the activities of adult Chioneas is derived partly from data recorded by others but largely from my own occasional observations of various species in the field and from observations of two dozen individuals of two North American species (*scita* and *stoneana*) and a smaller number of a Japanese species kept alive in the laboratory for varying lengths of time up to 19 days. To learn the details of the behavior of *Chionea* it will probably be necessary to devise an observation terrarium in which many individuals can be successfully maintained over a long period of time under conditions somewhat resembling those in their natural environment. This should include an underground cavity glassed on one side but shielded except during observations and provided with finely shredded, decayed wood or other such material as may be found in mouse nests in the ground. Provision should be made for temperature control sufficient to prevent overheating. I hasten to add that I have not constructed such elaborate quarters for the few Chioneas I have caged and watched, but my observations are only fragmentary and could have been much improved by an arrangement such as that described.

Observations of *Chionea* above ground—that is, on the snow or some artificial substitute for it—reveal only a fraction of the adult insect's total activities. This, of course, may prove to be the major fraction, but whether adults of *Chionea* are essentially inactive when underground or otherwise in darkened surroundings remains to be learned. When caged without access to places of concealment, Chioneas spend long periods of time virtually motionless, both by day and by night. When thus at rest they assume a characteristic posture (Fig. 50) in which the legs are drawn up more or less vertically against the sides of the body, the tibiae closed against the femora, and the tarsi beyond their basal segments appressed to the ground in a somewhat radiating pattern, so that the insect is suspended with its venter only slightly off the substratum. While in this resting position, the flies often raise and lower the body slowly and rhythmically by moving the folded legs first outward with the feet in place, then inward, so that the femora are once more against the sides of the body. This movement recalls (but does not resemble) the much faster, vibrating motions seen in some other limoniine species, notably in the subgenus *Geranomyia* of *Limonia*.

On several occasions I have observed a defensive behavior in *Chionea*. When moderately alarmed, the fly draws its legs close together above the body in a way that resembles the resting posture just described. The legs, however, are held even closer together and inclined backward, the femoro-tibial joints nearly in contact. This is probably the posture observed by Blurton (see Treherne, 1920: 201), who noted that *Chionea alexandriana* when approached would ". . . crouch down . . . as if it could feel the vibrations in the snow made by the weight of my snowshoes." In this position the fly stands motionless until the source of alarm has passed. This is probably its most effective means of avoiding such dangers as predation by birds, for with the legs drawn together above the body and somewhat laid back along the abdomen, the insect, seen from a few feet away, could well pass for a chip of bark or some other bit of darkly colored detritus such as one commonly sees on the snow in forested areas.

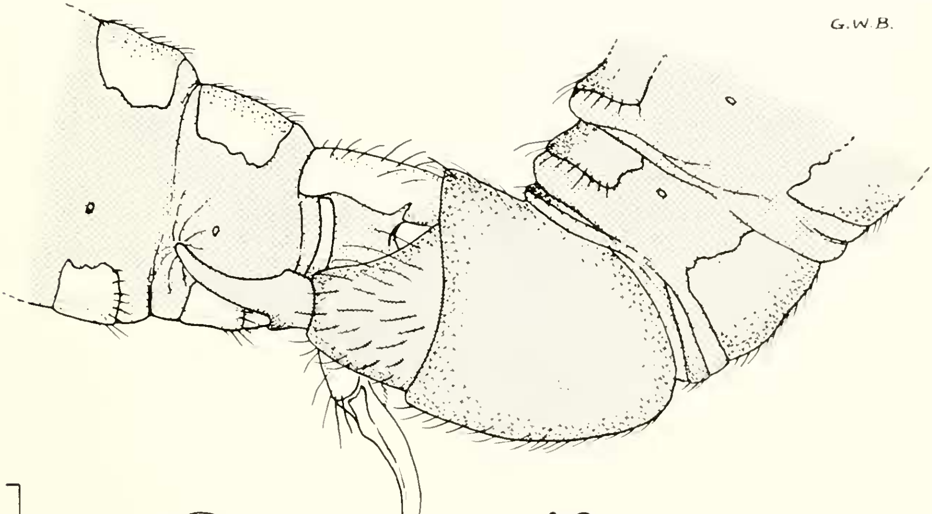
When greatly alarmed, *Chionea* ordinarily resorts to "running" or much less frequently to leaping. The running is actually a brisk walk, whereby the insect may move about four feet in a minute. I do not know whether females of *Chionea* are able to leap, but I have seen males jump distances greater than six inches (though usually much less). They sometimes jump without evident provocation, as in the case of a male of *C. scita* that suddenly leaped from the edge of a dish to the front of my shirt as I was watching its movements. Usually, however, *Chionea* jumps only in response to extreme alarm, such as when touched with a stick or other object. Females so stimulated did not jump.

Most often when Chioneas are encountered on the snow surface, they are walking with their characteristic, slow, deliberate gait. Their movements are not rapid and erratic, stop and go, this way and that, like those of so many other insects. In contrast, they proceed in an almost straight course over relatively long distances, treading the snow with such steady, rhythmic cadence and seemingly measured paces that they almost appear to be marching and to know where they are going. Watching the actions of *Chionea alexandriana*, Blurton (see Treherne, 1920: 201) was similarly impressed and wrote: "When travelling over the snow they always appear to be in a great hurry, and they move in nearly straight lines from one point to another . . . as if they had some special destination in mind." At this pace of about 80-100 "steps" per minute, *Chionea* can in that time travel 2-3 ft across the snow.

Marchand (1917) published a rather detailed account of the behavior of one individual of a European *Chionea* and from his observations arrived at some interesting conclusions about the species. He caged the insect in a glass box, the sides of which it climbed, and he interpreted this activity as a demonstration of negative geotropism. When the box was covered at each end by panes of glass, with a screen cover in the middle, and the *Chionea* repeatedly came to rest upon the screen, Marchand saw in this an attraction to cold temperature, or negative thermotropism. In both these instances, however, it seems the insect might merely have been trying to get out of the box. Marchand believed that the Chionea's retreat from his approaching hand was a reaction to heat, and he gave no consideration to the possibility that a human hand might have somewhat the same effect on a tiny insect as the approach of some predator. Some of Marchand's other conclusions were that *Chionea* must keep moving over the surface of the snow because it might freeze if it stops, that because one time the fly was observed walking into the wind the species may be positively anemotropic, and that exposure to sunlight caused the death of a *Chionea*.

I have not observed living Chioneas sufficiently to discuss most of Marchand's conclusions, but one of them—that *Chionea* is positively phototropic and is attracted to brightly illuminated snow—is in general contrary to my observations and ought to be examined. While watching adult Chioneas under the microscope, I noticed that they rather consistently avoided the light. This, of course, could have been a reaction to heat, although I was using cooled illumination. To explore the matter, I made a small house of cardboard with a door only large enough to let the insects pass in and out, and set this in the covered glass dish in which a male and a female of *Chionea scita* were kept. After three hours both flies were still sitting motionless outside the house. By 8:30 the next morning, however, the female was inside, and by 10:00 the male also had gone in. Thereafter, for eight days (after which observations were discontinued), the general pattern of their behavior was that the flies went into the house during the brighter hours of the day but were often outside in early morning, in the evening, or at other times of day when the sky was very cloudy. During these observations the flies were subjected to fluctuating outdoor winter temperatures on the north (shaded) side of a building in southern Michigan. Subsequently, it was my observation that *Chionea* is more likely to be found on the snow when the light intensity is reduced than in bright daylight. For example, I once searched several hours for *Chionea* in the afternoon of a clear day and found none. But as the sun sank low over the mountains and the shadows lengthened, several individuals of *Chionea* appeared in the very places I had sought them earlier in the day. Occasionally I have found them still on the snow surface after nightfall. I asked some other entomologists (John A. Chapman, William S. Osburn and David V. Durbin) to note light conditions at the time of capture of *Chionea*, and again—although not without exception—the flies were found late in the day, at evening, or on cloudy days, occasionally in early morning or during a snowfall. To this evidence could be added the similar observations of Lugger (1896: 230) and the capture of *C. scita*, *C. alexandriana* and *C. valga* in caves and of *C. stoneana* in rodent burrows. There are, however, two interesting pieces of apparently contradictory evidence. In Carbondale, Illinois, Dr. John Downey found a male of *C. stoneana* climbing the outside wall of a house, apparently attracted to a porch light, at about 11:00 p.m.; and in University Park, Pennsylvania, Dr. C. W. Rutschky collected a female of *C. scita* on a window screen, possibly attracted to light, again about 11:00 p.m. Perhaps, however, there is no real conflict between these observations, for it is quite possible that *Chionea*, like so many kinds of moths and other crepuscular and nocturnal insects more familiar to entomologists, is repelled by bright light, such as that of the sun during most of the day, but attracted to lights of low intensity.

I would agree with Marchand that the snow surface holds some special attraction for *Chionea;* that is, I do not believe its occurrence there is only coincidental. Although there is strong evidence that Chioneas are primarily underground insects, the great number of collections of them from the snow surface indicate the flies come there with some regularity and therefore very likely for some reason. Hågvar (1971) supposed that narrow limits of tolerance of temperature and wind led to the simultaneous appearance of numerous individuals of *C. araneoides* on the snow



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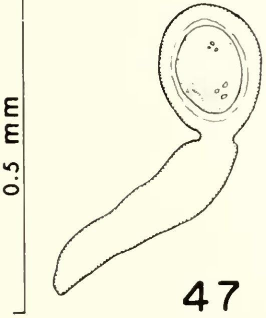

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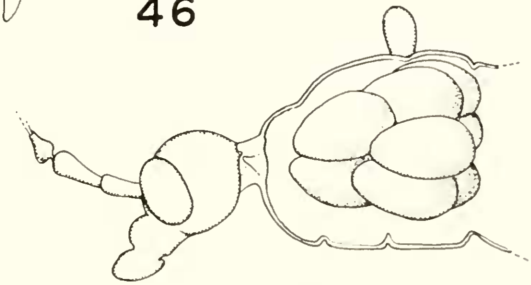

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Fig. 46, *Chionea jellisoni*, terminal abdominal segments of male (sclerites shaded) and female, to show relative positions during copulation. Fig. 47, cysticercoid of tapeworm, probably *Hymenolepis* sp., from abdominal cavity of adult female of *Chionea stoneana*. Fig. 48, *Chionea nivicola*, female, to show position of eight eggs in thorax in space made available by absence of indirect flight muscles. Scale: Fig. 47.

surface. Repeated observation of mating of the flies on the snow would support the suggestion of various authors that the reason is the bringing together of the sexes. It has also been suggested (Marchand, 1917: 150) that Chioneas are visually attracted to each other and find one another more readily because of the contrasting background afforded by the snow. It is true that they are conspicuous when seen from above against a white background, but if one scans the snowy terrain from a millimeter or so above the undulating surface—that is, adopts the insect's view of things—the idea of visual attraction becomes somewhat less convincing. Moreover, as discussed earlier under external morphology, the eyes of *Chionea* probably do not afford much visual acuity.

To say that the flies come out onto the snow surface so that males can find females is not a very thorough explanation of their presence there. Where *Chionea* has been found anywhere except on snow, both males and females have ordinarily been taken together in restricted microhabitats such as mouse nests, cavities beneath logs or rocks, in caves, rodent burrows, abandoned wasp nests, etc. Surely they are able to locate one another in such confined places. It occurs to me, however, that since *Chionea* is an insect of low vagility as compared to winged tipulids, and since it does live in groups (probably the progeny of one female) in partially isolated or restricted pockets, there might develop a degree of inbreeding detrimental to the species unless there was some device for bringing about a mixing of genes. Among winged Tipulidae reaching the adult stage in warmer weather, this may be accomplished by mating swarms (in which, of course, there still may be some inbreeding), or by more or less random flight by one or both sexes prior to mating. I regard the appearance of *Chionea* on snow as partly, at least, a means of effecting genetic recombination. Certainly, the relatively smooth surface of snow is less of an impediment to the movement of strictly pedestrian insects in search of mates than would be vegetation at the soil surface whether snow-covered or not. In addition, it is known that *Chionea* is a strong walker and may cover substantial distances; accordingly, wandering over the snow is probably important to the distribution of the flies into new microhabitats.

Mating Behavior

Several entomologists have commented on the rapid reaction of males and females of *Chionea* to each others' presence when placed in the same container. Lugger (1896), for example, observed that when a male and female (probably of *C. stoneana*) were caged together ". . . the snowflies immediately mated, notwithstanding it was several degrees below the freezing point." When I placed two males and two females of *C. scita* in a large vial lying on its side, in the field, they formed two mating pairs almost at once. These pairs separated during the return trip to the laboratory, but soon after the flies were put into rearing dishes they mated again. During the first three days after capture these same pairs of flies mated at least once daily, again on the fifth and sixth days, and once more on the eighth day. No mating behavior was seen thereafter; however, I was observing the flies only occasionally and probably failed to note all matings. Duration of mating was about 30-70 min but may be much longer.

On the basis of my observations of four species of *Chionea*, I can state that mating behavior is essentially the same in all. The male approaches the female ordinarily from behind, rising high upon his legs as he does so, with his body oriented almost vertically. His abdomen is then curved forward so that the hypopygium can grasp the female's ovipositor. But instead of facing in opposite directions during copulation, as is usual among crane flies that mate while standing on a surface, with one or both partners' abdomen rotated, both flies face in the same direction with the male's abdomen curved so that the hypopygium is inverted to achieve the usual tipulid arrangement, that is, with the male genitalia rotated 180 degrees in relation to those of the female (Fig. 49). Mik's description of the mating behavior of a European species of *Chionea* agrees with this (Osten Sacken, 1887: 196).

The male's dististyles secure a grip in the pleural membrane of the female's abdomen just cephalad from the strongly sclerotized eighth tergum. The hypovalves of the female are inserted beneath the male's ninth abdominal tergum, which deeply indents his membranous tenth segment, and the curved cerci are directed upward between his outspread basistyles (Fig. 46). Although the male's fore and middle legs touch the substrate during mating, it is the hind legs that must carry his weight and brace him against the female in this copulatory stance.

Males occasionally approach other males in the manner described above, suggesting a strong visual orientation to general shape and motion (but a lack of visual acuity) and perhaps the absence of chemical attraction in *Chionea*. Such encounters, however, are always brief.

Mating, as other activities of adult Chioneas, may take place at nearly any time of the day and under slightly subfreezing conditions. I have observed it more often at temperatures from 0-2°C (about 32-35°F) and at times of low light intensity, particularly late in the day.

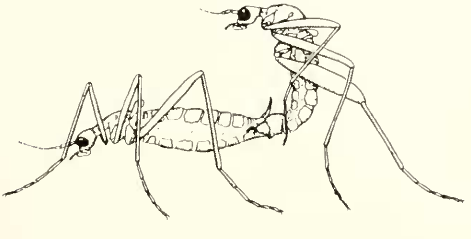

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FIG. 49, mating pair of *Chionea scita*, showing typical posture, with male supported chiefly by his hind legs.

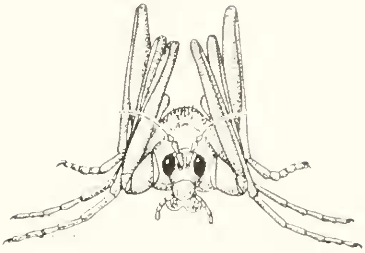

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FIG. 50, *Chionea scita* in resting posture, frontal aspect.

Parasites and Predators

Two kinds of helminths have been found associated with North American species of *Chionea*. In a series of *C. stoneana* from a mouse nest in eastern Kansas, I found cysticercoids of a species of tapeworm (Platyhelminthes, Order Cyclophyllidea) in the abdominal cavities of two out of three specimens dissected. These (Fig. 47) closely resemble the cysticercoid stage of *Hymenolepis* but have not been authoritatively identified. Ten were found in a male specimen in which the viscera were only slightly reduced in volume, but in a female containing 31 cysticercoids (28 in the abdominal cavity and three in the thorax), there were no eggs, although the spermathecae, appeared of normal size and contained closely packed spermatozoa. It is, of course, possible that she had laid all her eggs, though this seems unlikely, considering the condition of the other individuals collected at the same time. *Hymenolepis diminuta*, a common and widespread parasite of mice and rats, has been shown to pass its immature or cysticercoid stage in a variety of insects, including meal moths and their larvae, earwigs, *Tenebrio* grain beetles, *Tribolium* flour beetles, and larval fleas (Cheng, 1973). The insects become infested by eating eggs of the worm in the feces of the primary host and ingestion of the parasitized insects in turn serves to reintroduce the larval worms into the rodent, completing the cycle. From this evidence it seems reasonable to infer that whatever sort of mouse made the nest shared by *Chionea stoneana* (probably *Peromyscus leucopus*) is also an occasional predator on the fly. It is possible, moreover, that *Chionea* is often the intermediate host of such tapeworms among species of mice that in winter have no access to such indoor insects as those enumerated above (the flea being an exception). The type specimens of *Chionea stoneana* were found in nests of the meadow mouse or vole, *Microtus ochrogaster*, in Illinois; and in northern California *C. alexandriana* was found in an abandoned nest of the pack rat, *Neotoma* sp. (not identified at the time but probably *N. cinerea*, according to Dr. Robert Hoffman). There are also a few records of European species of *Chionea* from nests of rodents (see Bezzi, 1919). It must be that the eggs of the tapeworm are eaten by the *Chionea* larvae, since adult Chioneas probably take no solid food; and this knowledge offers some information about the larval diet.

In the case of the second helminth associated with *Chionea*, the relationship is apparently not one of parasitism but rather of phoresy. The worm is an unidentified species of nematode. At first glance an affected fly appears to have the neck membrane swollen, but closer examination reveals that there is a ring-like capsule around the neck, thin walled and somewhat the shape of the inner tube of an automobile tire (Fig. 51). It is not attached to the insect and often can be rotated on the neck by the tip of a needle, yet it fits very closely and cannot be slipped off over the head. Within the capsule are a large number of immature nematodes, which after a time rupture the capsule wall and emerge. Although I have seen only preserved specimens, they show various stages of increasing development of the nematodes within the capsule and then of their leaving it. The only suggestion that these worms might enter the body of the fly comes from the rare discovery of a few nematodes clinging to the thoracic sternum or about the leg bases of Chioneas with a half empty capsule around the neck or with no capsule remaining. None of these nematodes, however, has been found to have actually penetrated the fly's exoskeleton.

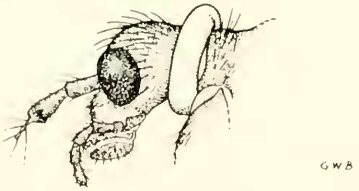

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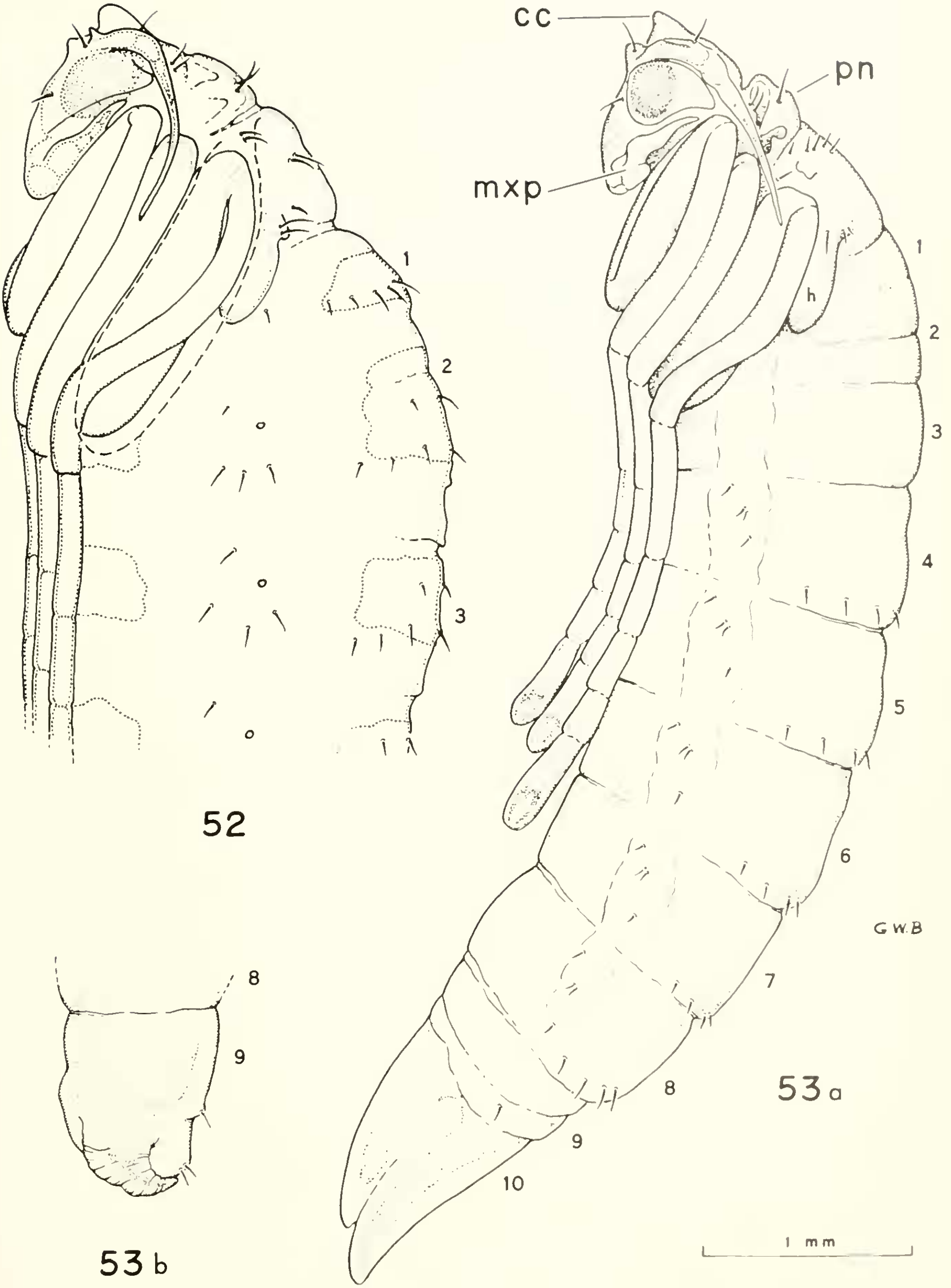
Fig. 51, *Chionea alexandriana* with egg case of nematode around its neck.

Dr. May Belle Chitwood (pers. comm.) determined that these nematodes are closely related to *Rhabditis*, some species of which are known to utilize insects as "hosts" for the purpose of transportation. In a discussion of the family Rhabditidae (order Rhabditata), Cheng (1973: 623) mentioned that parasitic forms of these nematodes may depend upon coprophagous insects to carry them from one host food source to another. It is possible that *Chionea* is used by the nematode as a means of travelling from one mouse burrow to another in order to parasitize the rodents. Or the *Chionea* may be merely a device for providing the nematode a generally more widespread distribution, if it is a free-living form. In any event, the female nematode probably places her egg capsule (which may be a more solid, gelatinous ring at the outset) around the fly's neck at the time of its emergence from the pupal skin, for it is at that time that the fly is least mobile and least able to avoid such treatment. I have speculated freely in the interpretation of these nematode capsules, but whatever the true story, it must be a very interesting one.

By attaining the adult stage in winter, *Chionea* escapes many of the common



Figs. 52-53, pupae of *Chionea*. 52, anterior portion of pupa of *Chionea alexandriana* (from California), left lateral aspect, showing, by dashed line, position of transparent, empty wing sheath. 53, female pupa of *Chionea lutescens* (from Denmark), left lateral aspect; cc—cephalic crest, h—haltere, mxp—sheath of maxillary palp, pn—pronotum, numerals indicate abdominal segments. 53a, cauda of male pupa of *Chionea lutescens* (from Denmark), left lateral aspect, showing relationship of pupal cuticle to genital structures of enclosed pharate adult. Scale only approximate for Fig. 52.

warm-weather predators that take a heavy toll of winged crane flies, such as spiders, dragonflies, asilids and ants among the invertebrates, and frogs, toads, salamanders and many kinds of birds among the vertebrates. One would expect, however, that winter birds foraging on the snow must sometimes pick up these flies, for they probably appear as conspicuous to birds as to humans. Occasionally, also, a small mammal might consume an adult *Chionea* while hunting on the surface of the snow, although I imagine mice would find the flies more readily in their burrows and nests. The only observation of predation on *Chionea* known to me is that reported by Pritchard and Scholefield (1978). They found that *Chionea obtusa* was commonly preyed upon by *Grylloblatta campodeiformis* (Insecta: Grylloblattodea) in western Alberta, Canada. This was determined both by direct observation in laboratory terraria and by recovery of recognizable fragments of *Chionea* among the gut contents from 23 dissected specimens of *Grylloblatta*. As discussed earlier, mice must feed on adults of *Chionea* to perpetuate the life cycle of the *Hymenolepis*-like tapeworm.

Most kinds of Tipulidae are plagued by parasitic mites, which sometimes may become so numerous as to have a debilitating effect on the host. In contrast, Acarina are extremely rare on *Chionea*. In fact, I have seen only one infested fly—a male of *Chionea nivicola* from near Moscow, Idaho, collected on snow, 8 December 1961, by R. E. Stecker. In this fly there was no evidence of general weakness, but numerous blackened patches were noted on the membranous areas of the anterior sternal region of the abdomen, near where the mites were attached. Eight of the mites were clustered just behind the coxae of the hind legs, but one had its mouthparts embedded in the pleural membrane of the second abdominal segment. These mites have been identified by Dr. R. W. Strandtmann (pers. comm.) as belonging to the genus *Arctoseius* (family Ascidae). This mesostigmatid genus has been recorded from a few northern localities, its species in every case heretofore described as free-living, occurring in soil and litter. There is no question, however, that the mites described here were attached by their mouthparts to the fly.

IMMATURE FORMS OF CHIONEA

Eggs, larvae and pupae of *Chionea* have only rarely been found anywhere the genus occurs, either in Eurasia or North America. Although I have obtained eggs from two American species, and from these the first instar larvae, and have once found older larvae, I have failed in every attempt to rear the insects. Immature forms of some European species have been described briefly, but no details of the life history of any species have been made known.

Prof. Kenneth W. Cooper, who has described many aspects of the biology of *Boreus*, the winter mecopteran, is the only one who has reared a North American *Chionea*. He plans to publish a description of its life history.

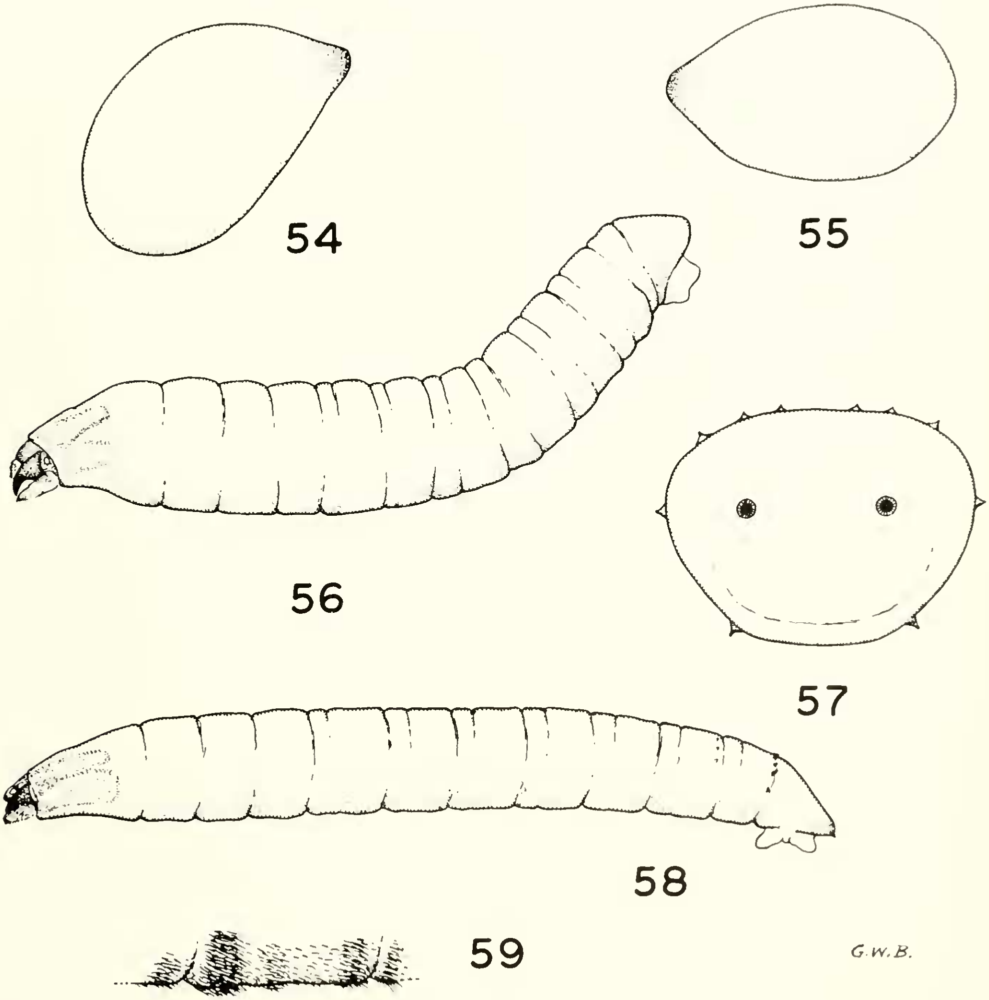
What follows concerning the immature forms of *Chionea* is offered to give at least a general impression of them.

Eggs

When laid, the eggs of *Chionea* are slightly elongate-ovoid, with an apparently white to pale buff color, which is imparted almost wholly by the contents, the chorion itself being hyaline, both transparent and glossy. The micropyle, or more exactly the microplyar area, is terminal, a little roughened, slightly protruding, fairly wide and sometimes pigmented (Figs. 54, 55). In the ovariole the egg is situated with the anterior or micropylar end away from the lumen of the ovary, and at the time of oviposition the more rounded posterior end of the egg proceeds first from the gonopore.

Although the largest eggs measured were from *Chionea valga*, a fairly large species, the smallest were obtained from *C. nivicola*, females of which have a greater average body size than those of *C. stoneana* producing slightly larger eggs. Dimensions of unlaid eggs of some representative species were *C. alexandriana*, 0.44 × 0.23 mm; *C. nivicola*, 0.43 × 0.22 mm; *C. scita*, 0.55 × 0.31 mm; *C. stoneana*, 0.45 × 0.27 mm; *C. valga*, 0.63 × 0.29 mm. Since egg size varies from one female to another in the same species and even somewhat among eggs of a single female, the above measurements actually are no more than averages for the particular individuals, yet they indicate the general size range for the genus.

During embryonic development there is a substantial increase in the dimensions of the egg, at least in those two species in which detailed observations of living eggs



FIGS. 54-59, egg and first instar larvae of *Chionea*. 54, egg of *Chionea stoneana*, lateral aspect; length 0.47 mm. 55, same, dorsal aspect. 56, *C. stoneana*, first instar larva; length 1.17 mm. 57, *Chionea scita*, spiracular disc of first instar larva, posterodorsal aspect. 58, *C. scita*, first instar larva; length approximately 1.2 mm. 59, *C. scita*, venter of typical abdominal segment, left lateral aspect, showing transverse bands of hairs (anterior at left).

were made. In *Chionea scita*, for example, the average dimensions increased from 0.55 × 0.31 mm to 0.63 × 0.36 mm, an increase of 15% in length and 16% in diameter. Probably the eggs take up moisture from their surroundings to bring about this change in size (cf. Torre-Bueno, 1920). To judge from the rapidity with which eggs of *Chionea* shrivel and collapse when separated from a moist substrate, the chorion must be readily permeable to water. Accompanying this increase in size is a change of color with age. Again, this seems to relate primarily to the darkening of the embryo as it takes on the characteristics of a larva, but there is also a slight increase in the faint yellowish or buff tinge of the chorion, tending toward pale amber-yellow, although the chorion retains its earlier transparency.

Duration of the egg stage was estimated by Brauer et al. (1854) as three weeks for the European *C. araneoides*. Under more or less natural conditions (outdoor rearing dish on a shaded widow-sill) in Michigan during late November and early December, when daytime temperatures fluctuated from 30-60°F, eggs of *Chionea scita* hatched after 15-18 days of incubation. Eggs of *C. stoneana* kept indoors but near a cold window-pane in January, in contrast, hatched after only eight days. Durbin (1975: 52) found that the incubation period in *C. carolus* varied from two to four weeks. From these scant data it would appear that the length of the egg stadium is, past a minimum time necessary for embryonic development, controlled largely by temperature and might be expected to fluctuate considerably in the natural environment, depending upon the winter weather of the year. Probably two to three weeks would be a reasonable estimate of the duration of this stage.

As the time of hatching draws near, the larva becomes increasingly active and may be seen moving within the egg. In *C. scita* this activity was noted during the last two or three days of the egg stadium. Since the chorion is transparent, the pigmented parts of the larva, such as eyes, mandibles, edges of cephalic sclerites and the like, and even the outlines of the rest of the body, are readily visible. The larva awaiting hatching rests most of the time but now and then may be seen "chasing its tail" around and around within the egg. As a result of this activity, the egg usually becomes rather shapeless just before hatching, changing form with the movements of the larva inside.

The number of eggs produced by one female varies according to the size of the individual (smaller females do not have proportionately smaller eggs) and probably also with the species. I have not dissected females of some species so cannot be sure of the latter. As mentioned earlier, a fully gravid female of *Chionea nivicola* contained 126 eggs, eight of them within the thorax (Fig. 48). A larger female of *C. alexandriana*, similarly bulging with eggs but without any crowded into the thorax, contained 194 and possibly had already laid a few when collected and preserved. A female of *C. scita* containing 132 eggs when collected had probably already laid some but still had a few within the thorax.

Just where the eggs are deposited in the natural habitat is not known, but possibly relevant observations were made of oviposition sites of two species in the laboratory. Both species were kept in covered rearing jars with moist paper tissue as the only substratum. *Chionea stoneana* females placed their eggs singly and always on the surface of the paper. Females of *C. scita*, however, almost invariably inserted their eggs singly into the paper tissue, usually just beneath the surface but in some cases to a depth greater than the length of an egg. Ordinarily the eggs were oriented with the anterior (micropylar) end upward. Twice I found an older egg (i.e., one that was expanded, with larval structures visible within) deeply placed but with a smaller, pale egg above it in the same hole. Either the two were placed at the same time, the second in each instance infertile, or the female returned to the hole considerably later and deposited a second egg. Age differences among the eggs, times of hatching, and numbers of eggs laid in comparison to the number retained by the females in each case indicate that oviposition is not accomplished by the deposition of large numbers of eggs in two or three days or nights, as has been observed in some short-lived, summer crane flies, but that it is prolonged over many days, the period of oviposition probably somewhat proportional to the long life of the female fly. It appears that in general the eggs are placed singly, in no particular area of concentration, and that in nature the female deposits an egg here and another there as she moves about over the soil surface or other loose material in the burrow of a small mammal or other underground cavity in which she is at the time residing. Lugger (1896: 230) describing the oviposition probably of *C. stoneana* (as *C. valga*), reported that after mating on the snow surface the female crawled into a crevice in the snow and "penetrating to some depth into the snow, she deposited a number of elongated eggs, which, however, did not hatch." Although mating often does occur on the surface of the snow, I doubt that eggs are normally deposited in snow but rather on or in soil, near some source of larval food.

Larvae

What little can be offered here concerning the larvae of *Chionea* is based in part upon the description of the larva of the European *C. araneoides* by Brauer et al. (1854) but mostly upon my own observations of the larvae of two North American species, *C. scita* and *C. stoneana*. Any generalizations about the larvae made in the following discussion must accordingly be taken with these limitations in mind.

Larvae of *Chionea* in all instars are characterized by: 1) elongate, terete form, without conspicuous dorsal or lateral lobes on the abdominal segments; 2) spiracular disc without dorsal or ventral marginal lobes; 3) head capsule well sclerotized, with broad dorsal and lateral plates; 4) hypostomal ("mental") bars of head capsule widely separated medially; and 5) sharply pointed, many-toothed mandibles. This combination of characters will serve to distinguish larvae of *Chionea* from those of all other tipulid genera by use of the best available keys (Alexander, 1920; Alexander and Byers, 1981).

First Instar Larva.—Upon hatching from the egg, the young larva of *Chionea* is short, thick, and nearly transparent, with rather diffuse sclerotization evident in the head capsule. Only the orange-brown mandibles and blackish margins of the dorsal and lateral plates are apparently well sclerotized, the rest of the head being light gray to light grayish brown. The integument is sparsely covered with fine, grayish pubescence, but because it is so transparent the viscera are plainly visible. The brain and ganglia of the central nervous system, for example, are large and conspicuous, as is the gut, and the slender dorsal tracheal trunks can easily be made out. After a few hours of larval life, the head capsule darkens, and the body becomes more elongate and somewhat yellowish, yet it retains most of its transparency.

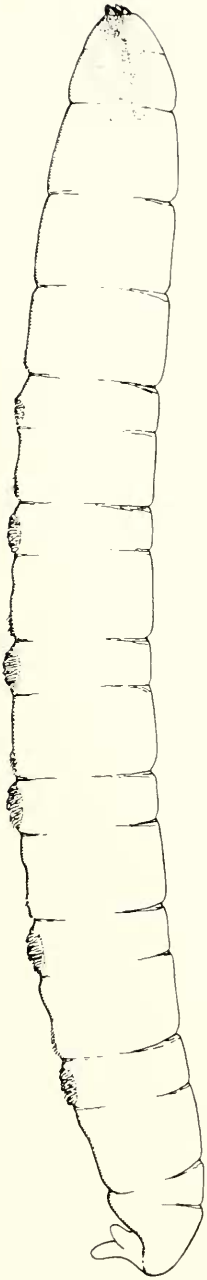
A newly hatched larva of *Chionea scita* measured 1.3 mm, or about twice the length of its egg just prior to hatching. This seems to be the usual ratio of body length to egg length at hatching. Growth is rapid, however, and four hours after hatching a larva of *C. stoneana* (Fig. 56) measured 1.17 mm, or 2.6 times the length of the egg just before emergence of the larva. The small relative size of the head capsule in the very young larva is noticeable. In a tipuline larva (*Dolichopeza;* see Byers, 1961*b*: 725, Fig. 79) two days old, the head capsule comprises about one-fourth of the total body length, but in a larva of *Chionea stoneana* of similar age it is only about one-seventh of the total length. The head structure of the first instar larva in general resembles that of an older larva, even the antennae and mouthparts being little different. The mandibles are more slender and the maxillae are somewhat more prominent. The integumental hairs in *C. stoneana* are very short and give the larva a roughened appearance, but those of *C. scita* are longer, especially ventrally (Fig. 59), and together with fine longitudinal plications in the skin itself impart to the larva a silky sheen in certain reflected lights. The caudal disc, or ninth abdominal tergum, of the young larva of *C. scita* (Fig. 57) is somewhat wider than long, shallowly impressed except around the edges, and bears two small, widely spaced spiracles. There are six minute, thorn-like projections arranged across the dorsal margin, the outermost ones slightly larger than the others, also two situated laterally and two ventrally. In the first instar larva of *C. stoneana,* the caudal disc is somewhat more deeply impressed, the spiracles slightly closer together, and the projections smaller, only the dorso-lateral and ventral pairs visible at the magnifications used.

During the final hours of the egg stage, when the larva is clearly visible through the chorion, the mandibles may be seen opening outward and closing inward and downward almost continuously, as if the larva were trying to bite its way out of the egg. It may be that some non-embryonic contents of the egg are ingested prior to hatching or that small fragments of the chorion are consumed during the larva's escape, for a few darkly colored particles may be seen within the gut of the larva as it is still emerging from its egg. The chorion, however, does not appear to be utilized even partially as the first larval meal, as in some other insects, but is left in a crumpled heap after the larva has emerged.

Young larvae of both *scita* and *stoneana* were not very active at temperatures from 36-52°F, but their activity increased with the rise in temperature within this span. They moved about to obtain food or to conceal themselves from light but at most other times lay still. Larvae of *C. scita* occasionally raised up with amazingly little of the posterior end of their bodies in contact with the moist paper substratum in their dish. In this position they were sometimes relatively motionless, at other times swayed slowly forward and backward

First instar larvae of *Chionea scita* were offered pulverized plant detritus for food but did not eat it. Since the mandibles were so sharp and the digestive tube so straight and without conspicuous caeca, unlike that of herbivorous tipulids, I thought the young larvae might be carnivorous. When I offered them a crushed podurid collembolan, they appeared to feed on it; however, the larvae died before growing noticeably, so I am unable to say what their diet was or should have been. Later observations on the diet of older larvae of *C. stoneana,* however, may be relevant and are discussed below.

Older Larva.—Two sizes of larvae of *Chionea stoneana* were collected from finely shredded material in an apparently abandoned mouse nest in eastern Kansas in January 1961. Despite their small size these are judged, on the basis of head capsule dimensions, to be the third and fourth instars. Six of the larger larvae average 5.8 mm in overall length and have a head width of 0.25 mm just behind the eyes; six of the smaller ones have a mean length of 4.3 mm and a head width of 0.18 mm. Head length is apparently too variable to use in differentiating instars, possibly because of increase during a larval stadium.



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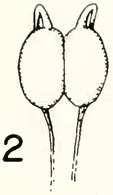

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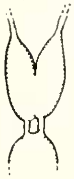

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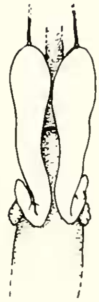

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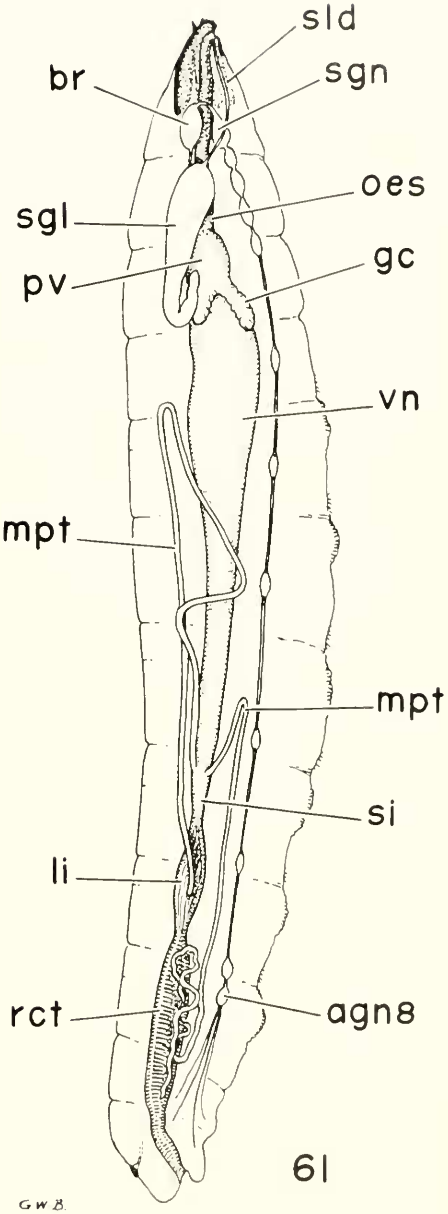

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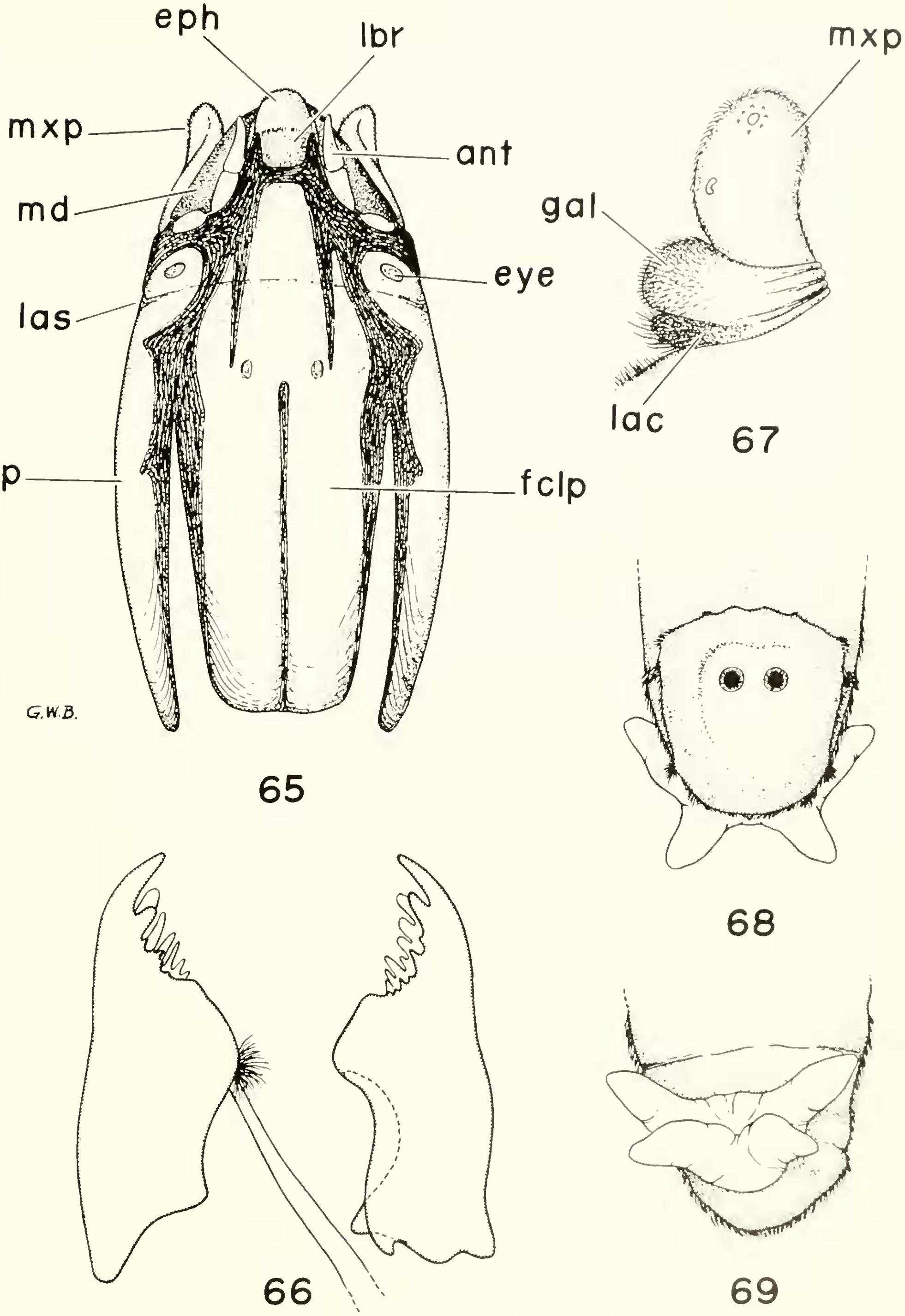
FIGS. 60-64, *Chionea stoneana,* larva. 60, larva (probably third instar), left lateral aspect; length about 5.9 mm. 61, internal anatomy of larva, right lateral aspect (skin cut on right side and partially outspread); agn8—eighth abdominal ganglion of ventral nerve cord (composite ganglion innervating posterior segments), br—brain, gc—gastric caecum, li—large intestine, mpt—malpighian tubule, oes—oesophagus, pv—proventriculus, rct—rectum, sgl—salivary gland, sgn—suboesophageal ganglion, si—small intestine, sld—salivary duct, vn—ventriculus. 62, brain, dorsal aspect. 63, suboesophageal ganglion and anterior half of prothoracic ganglion, ventral aspect. 64, salivary glands and portion of alimentary canal, dorsal aspect.

The ratio of growth from the smaller to the larger of these larvae, calculated from head width, is 1.4, and by application of this ratio, on the assumption that it is constant from one instar to the next, a head width of 0.13 mm can be calculated for the second instar. Further application of this "constant" yields a head width of 0.09 mm for the first instar, which is precisely that found by measurement. Accordingly, I consider the largest larvae found to be in the fourth stadium, and, because of their small size and the fact that some were preserved soon after molting, I would further conclude that they are in the early fourth stadium. If this conclusion is correct, considerable increase in body size during this stage would be required, for the largest larva in this group measured only 6.5 mm, and I would estimate a length of maturity of about 8 mm to yield an adult of 5 mm length, approximately the size in *stoneana.* In my study of *Dolichopeza* I found that there may be a 60% increase in larval length during the fourth stadium (Byers, 1961*b*: 747, Fig. 99); thus, a *Chionea* larva 6 mm long early in the fourth stage may well attain a length of 8 or 9 mm before pupation.

Third and fourth instar larvae are similar in appearance (Fig. 60), being elongate, nearly terete but slightly compressed, of approximately uniform thickness from the mesothoracic to seventh abdominal segment and tapered a little at each end. The body consists of a well sclerotized, almost completely retractile head, or head capsule, and three thoracic and ten abdominal segments. The prothoracic segment is weakly divided, its anterior ring concealed when the head is partially withdrawn. Both the mesothoracic and metathoracic segments, as well as the first abdominal, are undivided. Following these, each of the second through seventh abdominal segments is divided into a short anterior portion and a longer posterior annulus. The eighth segment is short and undivided. The tergum of the ninth or spiracular segment slopes steeply to the posterior end of the body; and situated on the underside of the wedge-shaped segment thus formed are the anal lobes, or "anal gills," which I believe represent the tenth or anal segment.

The integument is thin, soft, and densely covered with fine, yellow hairs, except on the pleural regions. Most of the hairs are so short as to be perhaps better described as pubescence, but on the venter they are longer, and on the lower surface of the anterior annulus of the second through seventh abdominal segments there is a transverse, slenderly elliptical patch of relatively long hairs that serves as a creeping welt. True creeping welts, however, are said by Alexander (1920: 795, in key) to be absent in the Tribe Eriopterini. On the dorsum, the longer hairs form narrow, transverse, poorly defined ridges, one on each undivided segment and two on the divided abdominal segments. A similar ridge appears ventrally on the posterior ring of each abdominal segment, recalling the pattern seen in the first instar of *C. scita* (Fig. 59). As the larva is turned while being observed under bright light, the fine, appressed integumental hairs present a silky sheen and straw-yellow color, and the pleural surfaces give an iridescent reflection. There are no setae or hairs of any greater size than those of the abdominal venter already described.

The spiracular disc is concave in the middle (Fig. 68) in the living larva and in most preserved specimens, but treatment of a larva with hot water for preservation may obliterate this depression. There are no conspicuous lobes surrounding the disc, yet one or two pairs of slight protuberances can be made out along its dorsal edge. Elsewhere about the perimeter are hairs, which form small tufts laterally at the level of the spiracles and ventro-laterally. The spiracles are circular with black centers. In *C. stoneana* there is no pig-



FIGS. 65-69, *Chionea stoneana*, details of larva. 65, head capsule, dorsal aspect; length 0.54 mm; ant—antenna, eph—epipharynx, fclp—frontoclypeus, las—line of attachment of skin, lbr—labrum, lp—lateral plate, md—mandible, mxp—maxillary palp. 66, mandibles, ventrolateral aspect of each (asymmetry due only in part to slight difference in position); length of right mandible, pictured at left, 0.093 mm. 67, left maxilla, ventral aspect; gal—galea, lac—lacinia, mxp—maxillary palp. 68, spiracular disc of fourth instar larva, posterodorsal aspect. 69, anal lobes, or "gills," of fourth instar larva, ventral and slightly lateral aspect.

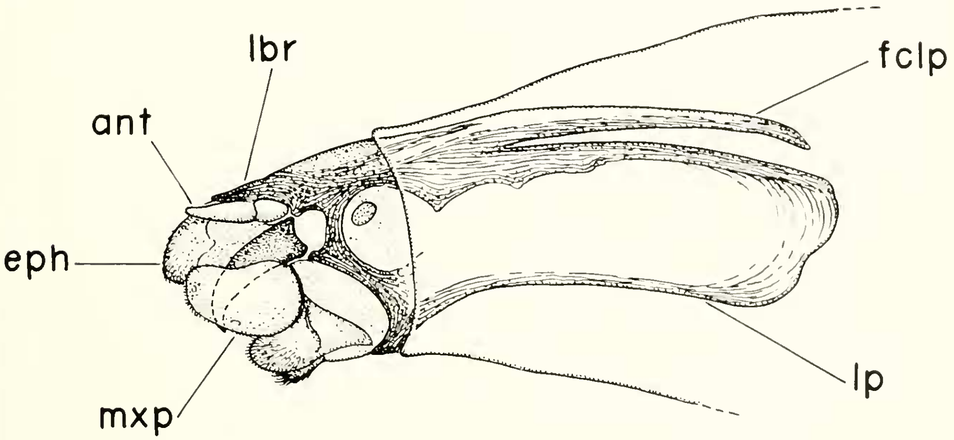
mentation above or between the spiracles, such as is found in the European *C. araneoides* (see Alexander, 1920: 952, Fig. 447) and *C. lutescens.* There are four retractable, subhyaline anal lobes (Fig. 69), the anterior pair somewhat longer than the posterior pair. It seems unlikely that these serve any respiratory function, so I would not apply the term "anal gills" to them. They may, however, aid in locomotion and may be withdrawn when the larva is quiescent.

Head and Mouthparts.—The resemblance of the larval head of *Chionea* to that of *Cladura* illustrated and described by Alexander (1922) is striking and gives strong support to the supposition of close relationship between these two genera based on the adult flies. At the same time, the head capsule in *Chionea* is unlike that of most other eriopterine genera (e.g., *Erioptera, Molophilus, Ormosia, Gonomyia*) in that it is extensively sclerotized. In place of slender bars or rods extending backward from the anterior region of the head, as in the typical eriopterine, *Chionea* has broad dorsal and lateral plates (Fig. 65), much like those seen in larvae of the Limoniini. The large dorsal plate (epicranial plate) I regard as the fronto-clypeus (Byers, 1961*b*: 734). Apparently formed from two areas of sclerotization, it has a median, blackened line of fusion of the two plates and is notched at the middle of its truncate posterior end but is not otherwise divided. The lateral margins of the fronto-clypeus are blackened and recall the strongly sclerotized, blade-like extensions of the lateral plates seen alongside the fronto-clypeus in some tipuline larvae. The lateral plates are slightly bowed outward but are not deeply concavo-convex. Their dorsal and ventral margins have a similar curvature and are more or less parallel, the posterior end of each plate being irregularly truncate. There is evidence that both the fronto-clypeal and lateral plates may elongate by accretion during a larval stadium and that the lateral plates may grow more rapidly than the dorsal one, but I have not made any comparative measurements on particular individuals to substantiate this.

There is a strong, rigid fusion of the fronto-clypeus with the lateral plates at each side for about one-third the length of the entire head capsule, but the lateral plates are not connected ventrally. The space between their lower margins is approximately oval, broadly open behind but partially closed anteriorly by the hypostomal bars. There is no hypostomal bridge (or "mentum," as it has been called), that is, no median sclerotization; the bars merely extend far enough to provide for the lower articulation of the maxilla, then terminate in a slightly widened, indistinctly toothed tip. The labrum (Fig. 65) is fused posteriorly with the fronto-clypeus and produced anteriorly into two darkly sclerotized points that project over the sides of the epipharynx. The epipharynx is rounded anteriorly, curved downward and narrowed ventrally, and is coarsely pubescent. Lying alongside the labrum and above the bases of the mandibles are the antennae, each consisting of a sub-cylindrical, apparently immovable basal segment and an elongate, conical terminal segment.

Each mandible is hinged along a rather short base, articulating dorsally with the strongly sclerotized clypeal region of the head just below the antennal base and laterally with a conspicuously projecting, blackened condyle close above the maxilla (Fig. 70). As the dorsal points of articulation are closer together than the lateral ones, the movement of the jaws is downward and inward, upward and outward, the tips touching or nearly so at full closure but not overlapping. The mandibles (Fig. 66) are sharply pointed, densely sclerotized, and blackened basally, with two rows of denticles on the mesal surface of the apical one-third of their length.

Some of the denticles are acutely tipped, others rounded, and the larger ones appear somewhat flattened and blade-like. Near its mid-length the mandible bears a bulbous mesal enlargement, within which the tendon of the mandibular adductor muscle is attached and on which a tuft of hairs (brustia) is situated. This enlargement possibly serves as a molar surface for grinding food, but there is no evidence so indicating, either in the nature of the surface itself or in the larval diet as far as it is known. In fact, the sharp tips and double rows of denticles on the mandibles suggest that the larva of *Chionea* may be carnivorous, certainly that it is not a typical herbivorous tipulid. There is considerable variation in the shape of the mandibles, as shown by Figure 66 which compares both mandibles of the same individual. Part of the evident difference in the basal portions of these two mandibles is due to slight rotation of one from the position of the other. Below the mandibles and largely concealing them in ventral aspect are the maxillae, which have a membranous attachment to the anterior margins of the lateral plates and to the hypostomal



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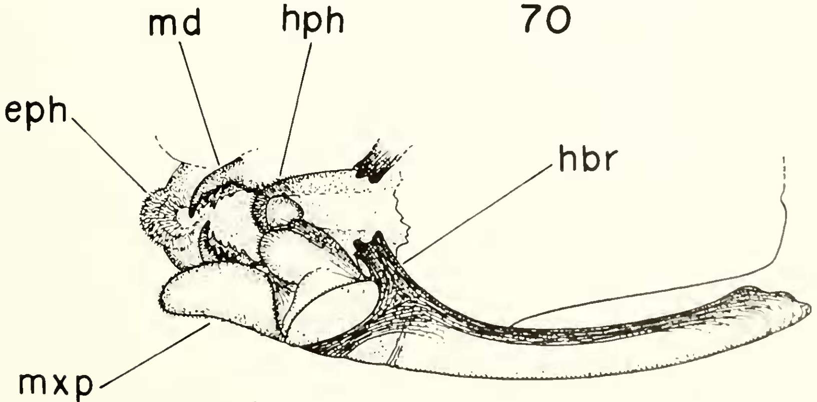

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FIGS. 70, 71, *Chionea stoneana,* head capsule of larva (probably third instar); length of head 0.54 mm. 70, left lateral aspect, showing anterior part of membranous cuticle attached; ant—antenna, eph—epipharynx, fclp—frontoclypeus, lbr—labrum, lp—lateral plate, mxp—maxillary palp. 71, ventral aspect (most of left half omitted); eph—epipharynx, hbr—hypostomal bridge, hph—hypopharynx, md—mandible, mxp—maxillary palp.

bars. The maxillae are large, fleshy (i.e., thick but lightly sclerotized), trilobed, and covered with minute pubescence (Fig. 67). The more dorsal lobe is the palp and has at its apex what appears to be a sensory apparatus, and the narrow, sclerotic band around its base is possibly the rudimentary stipes. The smaller, lower lobes very likely represent the galea and lacinia, and the sclerotized band traversing their common base may be all that remains of the cardo.

Ventrally, the mouth cavity is bounded primarily by the lower lobes of the maxillae (Fig. 71) and is closed medially by the combined hypopharynx and labium. The hypopharynx itself is well sclerotized and is connected laterally to the inner ends of the hypostomal bars. It is pilose on its dorsal surface, which slopes downward to a rounded anterior margin.

Near the anterior end of each lateral plate and behind the mandibular attachment, there is a subcircular clear area in the plate, bordered above, before, and below by intense sclerotization. In the living larva and in some preserved specimens, a dark spot may be seen beneath this clear area. This pigmented spot is the eye, which in life has the characteristic purple color and which can be moved about slightly beneath its cuticular covering.

Alexander (1920: 952, Fig. 445) drew attention to a peculiar structure on the dorsal surface of the head capsule illustrated by Brauer et al. (1854: Fig. 5). He interpreted this as a pair of "appendages which are toothed on the outer face" and concluded that "these probably represent part of the mentum, but from Brauer's figures they would appear to lie above the labrum." Brauer's illustration is confusing in certain respects but seems to me to be purely a dorsal view, the structures in question probably being the two halves of the fronto-clypeus.

Internal Anatomy.—Only the larva of *Chionea stoneana* was explored internally, so comparisons with other species are not possible at this time, except for a few minor comparisons with Brauer's figures of *C. araneoides* (Brauer et al., 1854: Figs. 3, 4). The larva illustrated (Fig. 61) was immersed in hot water, which resulted in its outstretched condition. In a living larva most of the organs are more contracted, thus are wider and not so linearly arranged.

Digestive system: The most conspicous structures inside the larva are those comprising the digestive tube (oesophagus, proventriculus, ventriculus, and intestine) and organs associated with it (salivary glands and Malpighian tubules). The oesophagus is a relatively straight, muscular tube of narrow diameter, leading from the mouth to the anterior end of the short, thick-walled proventriculus. Above and beside the proventriculus and oesophagus lie the two salivary glands (Figs. 61, 64), which have a large lumen; they are widest anteriorly, tapering and recurved cephalad posteriorly, with thin walls, formed of large, flattened, polygonal cells containing nuclei of such great diameter that they can easily be seen with the dissecting microscope at 130× magnification. In most of the larvae dissected the salivary glands were large and distended, and I have never seen salivary glands of such comparatively great size in any other crane fly larva. At each side of the anterior end of the ventriculus there are two elongate gastric caeca. These are twice as long in some individuals as in others, their length possibly varying with physiological activity, for in those specimens having the longer caeca there was a greater amount of food in the ventriculus.

More than 40% of the length of the digestive tube is the ventriculus which is muscular and relatively smooth-walled, its anterior half approximately three times the diameter of the posterior half. There are four Malpighian tubules attached two at either side of what appears to be the posterior end of the ventriculus, although they are anatomically behind the proctodeal valve. Sometimes these tubules appear to be arranged randomly in the haemocoel, but one or two may have their distal ends closely applied to the wall of the rectum, supposedly to facilitate the excretory function by fairly direct transport of recovered water. The small intestine and large intestine are poorly delimited, short and thin-walled as contrasted with the ventriculus. Notably absent from the hind gut is the intestinal caecum, which is conspicuous in all herbivorous tipulid larvae I have investigated. The rectum is longer than the rest of the hind gut and of greater diameter; it appears somewhat striated because of small bands of muscle in its nearly membranous walls.

Tracheal system: The dorsal tracheal trunks are of surprisingly small diameter (Fig. 72), which may relate to the rate of metabolic activity of the larva. Since the distribution of branch tracheae and other parts of the respiratory system in *Chionea* follows rather closely that described for *Dolichopeza* (Byers, 1961*b*; 740-741, Fig. 82), I have not illustrated the tracheal system in Figure 61 and will not describe it in detail here.

Central nervous system: Lying in the prothoracic segment just behind the head capsule and above the oesophagus is the brain (Figs. 61, 62). It consists of two broadly joined ellipsoidal lobes, each giving off a circumoesophageal connective anteriorly and a more slender posteroventral branch leading to the viscera. The suboesophageal ganglion is made up of two spindle-shaped bodies joined at the mid-line for somewhat over half their length (Fig. 63). Each of these receives a circumoesophageal connective at its anterior end and is joined posteriorly by a short length of the nerve cord to the first thoracic ganglion. All three thoracic ganglia lie generally in the floor of the larval mesothorax. The eight abdominal ganglia

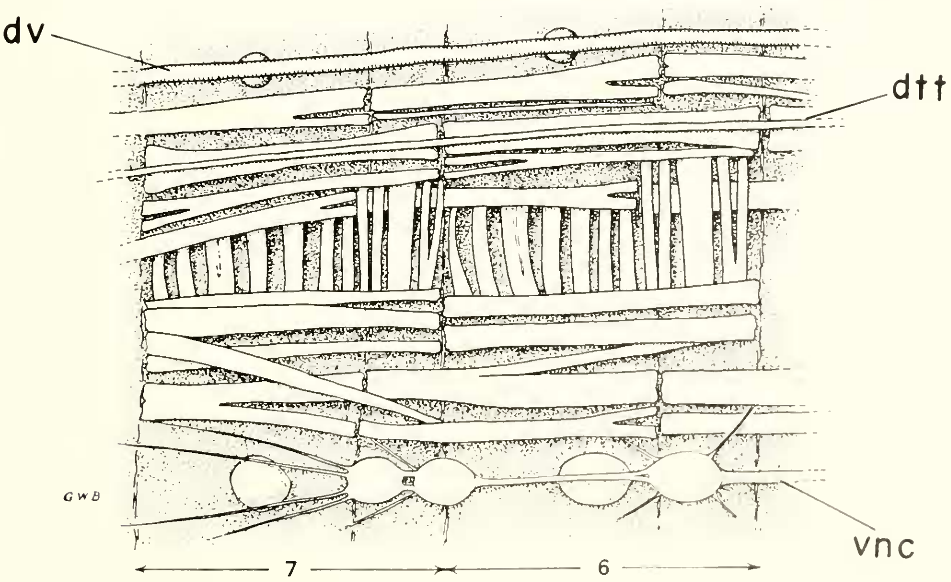


Fig. 72, peripheral musculature, nervous, circulatory and respiratory structures in sixth and seventh abdominal segments of larva of *Chionea stoneana*, interior aspect; approximately half of each segment shown, from near mid-dorsal line above to near mid-ventral line, anterior at right, extent of segments indicated by numbered arrows at bottom of drawing; abdominal ganglia 6-8 shown; dtt—dorsal tracheal trunk, dv—dorsal vessel, vnv—ventral nerve cord.

are arranged from metathorax to seventh abdominal segment, as shown in Figure 61.

Muscular system: Figure 72 will give some impression of the complexity of number and arrangement of the muscles of the body wall in two representative segments of a fourth instar larva. These muscles were not studied in detail. Their functions can be inferred from their points of attachment. Longitudinal muscles, both intersegmental and intrasegmental, are concerned largely with locomotion. Both vertical and longitudinal muscles occur in the pleural region and probably function both in locomotion and in deformation of the segments for other purposes, such as displacement of haemolymph.

In Figure 72 it may be noticed that beneath the nerve cord, near mid-length of each segment, there is a circular or subcircular structure. A similar but smaller disc occurs in the dorsum of each abdominal segment, above the dorsal vessel. These whitish, flattened structures, closely applied to the body wall, are of unknown function; they are not to be confused with histoblasts of legs and wings that may be seen in the thorax of crane fly larvae. Their gross anatomy suggests they may be glandular.

Pupae

The pupae of only two North American species of *Chionea* have been found, but none has yet been described. As mentioned earlier, K. W. Cooper will describe the immature forms of *C. valga*. In October 1975, David Durbin found one male and two female pupae in hard, compact soil in rearing dishes in which adult Chioneas had been kept 8-9 months earlier (Durbin, pers. comm.). The species could not be determined with certainty but was probably *C. alexandriana* Garrett. Mr. Durbin kindly permitted me to examine two of these pupae in order that I might compare them with pupae of *C. lutescens* Lundström, a European species. Edwards (1936: 89) briefly described pupae of *C. lutescens* from Denmark and compared them with the description of the pupa of *Cladura* by Alexander (1922). I have examined these pupae (Byers, 1961*a*) and in the following paragraphs compare them with Durbin's specimens from California.

Since the overall dimensions of the pupa bear a fairly direct relationship to the size of the developing adult within, one would expect the pupae to show variation in size similar to that seen among adults. Moreover, since in the pupal instar the body is not greatly contracted, or telescoped, the pupa may be expected to be somewhat longer than the adult. The pupae of both *Chionea lutescens* and *C. alexandriana* are about 6-7 mm in length as preserved in alcohol. Their color late in the pupal stadium is light brown, the pupal skin itself nearly hyaline and the pupal color largely that of the developing imago. There is probably considerable darkening of the body of the enclosed adult during the day or so just prior to its emergence, producing a corresponding apparent color change in the pupa with only slight darkening of the pupal skin.

Head.—The cephalic crest (Fig. 53, cc) is prominent, arching forward to a narrowly rounded apex, then descending abruptly on its anterior surface. It is shallowly grooved along the dorsal mid-line and bears a large seta posteriorly at each side. Over the basal segment of each antenna there is a rounded lobe with a seta near its apex. The part of the antennal sheath enclosing the pedicel is roughly cylindrical, then there is a slight enlargement of the sheath to accommodate the fusion segment, and thereafter it tapers evenly to the tip. Edwards (1936) expressed surprise at the length of the antennal sheaths but overlooked the fact that the flagellomeres have unusually long verticils. Sometimes the distal end of the antennal sheath lies alongside the anterior or middle tibia instead of in the position illustrated, but the proximal portion is close above the pupal eye. Rounded above and below and somewhat flattened mesally, the pupal eye has a broadly triangular, lateral prolongation that extends well beyond the adult eye developing beneath it. Such a prolongation occurs in pupae of several eriopterine species. It is considerably wider in *Chionea* than in the closely related *Cladura* (cf. Alexander, 1922: Fig. 7). Near the mesal margin of each pupal eye is a seta, apparently on the frons, although the frons, clypeus and labrum are joined without evident sutures. The sheaths of the maxillary palps and labellar lobes of the labium are distinct, those of the palps being more or less straight and lying alongside the anterior margins of the sheaths of the front legs.

Thorax.—Absence of evident wing sheaths and respiratory horns is the most conspicuous aspect of the thorax (Fig. 53). Actually, however, there are flattened, closely appressed, wholly transparent—and of course empty—wing sheaths, approximately overlying the metathoracic femur and tibia, as indicated by a dashed line in Figure 52. I am indebted to David Durbin and Kenneth Cooper for pointing this out, for I had overlooked these structures on the pupae of *C. lutescens* (Byers, 1961*a*). Nevertheless, I believe that the reference by Edwards (1936: 89) to "small wing sheaths" in that European species must pertain to the sheaths of the halteres, for the surprising fact about those of the wings is that they are of what might be called full size, that is, proportionately as large as in the fully winged *Cladura*. It is something of a puzzle why they have persisted at all when other evidence suggests that the essentially apterous condition of the adults is an ancient one. The sheaths of the halteres are closely applied anteriorly to the sheaths of the hind legs and mesally to the first abdominal segment.

Wood (1952: 106) similarly found no great difference in size of wing sheaths between subapterous and fully winged species of South African *Longurio*.

In view of the close similarity of the pupae of *Chionea* and *Cladura* (Alexander, 1922) in other features, the absence of thoracic respiratory horns in *Chionea* is not too surprising. In their place are a pair of small, narrow, curved pits, one at either side on the anterior mesonotum (i.e., in front of the pseudosutures). These incisions should not be confused with the pit-like depressions at either side of the pronotum. Setae are distributed on the pronotum, mesonotum, and bases of the sheaths of the halteres approximately as illustrated in Figures 52 and 53. Their lengths and positions vary between species and somewhat from one individual to the next within a species.

The leg sheaths are situated generally as shown (Fig. 53), although their arrangement varies in detail. There appears to be considerable contraction of the femora and tibiae within their respective sheaths which are relatively short, extending backward only to the second abdominal segment. The femoral sheaths are folded, somewhat basad from mid-length, thereby providing some additional space for development of these conspicuously elongate segments. This can be most easily seen in the prothoracic legs, viewed from below. In contrast to the short leg sheaths, those of the tarsal segments, except the basitarsi, have a length rather close to that of the corresponding segments in the emerged adult, and there seems to be comparatively little contraction in the tarsi prior to emergence. The sheaths of the front and middle legs extend to about the posterior margin of the fifth abdominal segment, those of the hind legs to the posterior edge of the sixth abdominal segment. Toward the end of the pupal stadium the tarsi are readily visible within their sheaths and are partially rotated so that their dorsal surfaces are directed laterally with respect to the body of the pupa.

Abdomen.—The first abdominal segment is short and undivided as in the larva. In a young pupa (Fig. 53) only the second segment has a fairly distinct, short anterior ring and a longer posterior one, the third through seventh segments being very weakly divided, although the constrictions between segments are distinct. By the time the adult insect is well formed and its cuticle has separated from the pupal cuticle (the pharate condition), the pupal segmentation is almost obliterated but is indicated by the visible adult sclerites (Fig. 52). While abdominal spiracles are not evident on the pupa (Fig. 53), those of the developing adult eventually become clearly visible through the pupal cuticle (Fig. 52). In the female both the tenth segment and the cerci are contained within the tergal sheaths of the ovipositor, while the sternal sheaths, continuous with the sternal region of the eighth segment, enclose the hypovalves of the developing adult. In the male (Fig. 53a) there is an indistinct constriction near mid-length of the ninth abdominal segment which can, as the adult body separates from the pupal skin, be seen to correspond to the division between the basal portion of the segment and the styles, particularly the basistyles. The dististyles are formed within thick, wrinkled or striated, irregularly tapering sheaths that curve upward at the extreme end of the pupa. When the adult body is almost fully formed, the genitalial structures, which earlier had become distinctly separated from their sheaths, do not nearly fill them, but the rest of the imaginal abdomen remains tightly pressed against the pupal skin.

The distribution of setae on the pupal abdomen varies with species as indicated in Figures 52 and 53. Near the posterior edge of the third through seventh terga there is a transverse row of eight short setae. One or two pairs may be present in a more anterior transverse row on these terga, or there may be no others. The pleural regions are only slightly raised, with four minute setae arranged as in the figures, occurring at each side on the second through seventh segments. On the posterolateral eighth or anterior ninth segment there is a single short bristle at each side. All these setae are much less prominent than their counterparts in the pupa of *Cladura flavoferruginea,* and certain of the setae found in that species are lacking in *Chionea.* There are no setae on the sterna in either males or females.

Usually the pupa frees itself of the last larval skin, but Kryger (see Edwards, 1936: 90) found one pupa of *C. lutescens* with the larval skin still attached.

KEY TO MALES OF NORTH AMERICAN *Chionea*

1. Body color light yellowish brown; antennae with 9 or more flagellomeres (sometimes 8 in *albertensis*) including fusion segment 2

   Body color brown, reddish brown, gray or black; antennae with 7 or fewer flagellomeres (rarely 8 in *obtusa*) 5

2. Posterior margin of ninth abdominal tergum entire, without setiferous lobes and not notched (Fig. 99) 3

   Posterior margin of ninth abdominal tergum with 2 setiferous lobes and an intervening U-shaped or V-shaped, pale, membranous area (notch in tergal margin) (Figs. 75, 231) 4

3. Dististyles spatulate, broadly rounded at apex, concave on mesal surface (Fig. 222); abdominal terga with median spot and darkened lateral margins .... *wilsoni,* new species

   Dististyles not spatulate, pointed at apex, of about same diameter throughout, beyond base (Fig. 99); abdominal terga without distinct color pattern .... *scita* Walker

4. Gonapophyses in dorsal aspect narrowing gradually toward posterior apex (Fig. 75); setae of body and legs acuminate, hair-like; notch between lobes of ninth abdominal tergum broadly to narrowly V-shaped (Figs. 75, 80) *albertensis* Alexander

Gonapophyses in dorsal aspect broad just before posterior apex, narrowing abruptly (Fig. 231); setae of body and legs thick, black, spine-like, those of hind legs with elevated bases (Fig. 230); notch between tergal lobes broadly U-shaped .... *macnabeana* Alexander

5. Gonapophyses slender, upturned and hook-like at apex (Figs. 157, 188, 195, 214) 6

Gonapophyses without slender, hook-like apex (Figs. 107, 117); small subapical tooth (Fig. 176) may be present 11

6. Dististyles with dorsal, pilose concavity on apical half (Fig. 186) .... *excavata,* new species

Dististyles without dorsal, pilose concavity 7

7. Gonapophyses bowed outward from base to near mid-length, then converging slightly in apical half, apices again divergent (Figs. 165, 204); antennae with 4 or 5 flagellomeres, including fusion segment ... 8

Gonapophyses not bowed outward, their inner borders in dorsal aspect only slightly diverging; antennae usually with 3, rarely 2 or 4, flagellomeres 9

8. Dististyles each with blackened ventral tooth; gonapophyses each with semicircular dorsal flange directed dorsolaterad; ninth abdominal tergum with shallow median emargination bordered by setiferous lobes (Fig. 204) .... *lyrata,* new species

Dististyle without ventral tooth; gonapophysis without dorsolateral flange; ninth tergum with deep, U-shaped emargination and without lobes (Fig. 165) *carolus* Byers

9. Body color generally black; sclerites with velvety texture, membranous areas dark gray (Fig. 214) .... *nigra,* new species

Body color generally brown; sclerites smooth except for hairs, membranous areas light brown 10

10. Abdominal terga darkened anteriorly and along mid-line, producing evident pattern; tergal hairs scattered over tergum, especially on posterior half; space between gonapophyses (dorsal aspect) usually narrowly U-shaped (Fig. 156) . .. . *alexandriana* Garrett

Abdominal terga unicolorous or nearly so; tergal hairs short, sparse, concentrated along posterior edges of terga; space between gonapophyses widest at base, narrowed near mid-length of gonapophyses (Fig. 193) .... *jellisoni,* new species

11. Antennae with only 2 or 3 flagellomeres; gonapophyses elongate, narrow, with sides of each subparallel or slightly converging 12

Antennae usually with 5 or 6 flagellomeres; gonapophyses broad or deep, blade-like, with one or both sides of each conspicuously curved and convergent toward apex 14

12. Posterior margin of ninth abdominal tergum appearing entire (dorsal aspect) or broadly and evenly emarginate (posterodorsal aspect); gonapophyses in dorsal aspect broad, concave on upper surface, with convergent apices (Fig. 110); antennae usually with only 2 flagellomeres; body color light brown to brown . *hybrida,* new species

Posterior margin of ninth abdominal tergum narrowly emarginate, with projecting, setiferous lobes bordering emargination; gonapophyses in dorsal aspect elongate, narrow, with subparallel sides; antennae usually with 3 flagellomeres . 13

13. Body coloration dark brown and light brown, with evident pattern on abdominal terga (Fig. 172); gonapophyses with small subapical tooth on dorsal margin, apices slightly convergent (Fig. 176) .... *durbini,* new species

Body coloration dark gray, without pattern on abdominal terga; gonapophyses without subapical tooth on dorsal margin, apices not convergent (Fig. 129) .... *stoneana* Alexander

14. Thoracic dorsum humped, anterior slope of mesonotum steep (Fig. 139); posterior margin of ninth abdominal tergum appearing entire (dorsal aspect) or broadly and evenly emarginate (posterodorsal aspect), without setiferous lobes (Fig. 141) .... *valga* Harris

Anterior slope of mesonotum gradual (Fig. 123); posterior margin of ninth abdominal tergum with broadly V-shaped emargination and low, broad lobes or narrow lobes bordering emargination 15

15. Gonapophyses in form of vertical plates, divergent at base (Fig. 89), convergent apically; posterior margin of ninth abdominal tergum with narrow, prominent lobes bordering emargination (Fig. 88) .... *nivicola* Doane

Gonapophyses each a broad, horizontal plate concealing vertical keel (Fig. 117); posterior margin of ninth abdominal tergum with low, broad lobes bordering emargination (Fig. 118) .... *obtusa,* new species

Key to Females of North American *Chionea*

1. Body coloration light yellowish brown; antennae with more than 8 flagellomeres 2

Body coloration brown, reddish brown, gray or black; antennae with fewer than 8 flagellomeres 5

2. Ninth abdominal sternum not interrupted medially, either with acute median angle and elongate, moderately sclerotized areas at either side of its mid-line (Fig. 82) or with subtriangular, moderately sclerotized median structure protruding ventrally (Fig. 228); arms of genital furca bowed inward or nearly straight, forming V-shaped figure 3

Ninth abdominal sternum interrupted medially, with subtriangular, moderately sclerotized area at either side of mid-line (Figs. 85, 105); arms of genital furca bowed outward, making U-shaped figure .. 4

3. Ninth abdominal sternum forming acute median angle (Fig. 82); western species .... *albertensis* Alexander

Ninth abdominal sternum forming subtriangular median structure that protrudes slightly ventrally (Fig. 228); species of southeastern U. S. .... *wilsoni,* new species

4. Stout black setae along posterior margins of sixth and especially seventh abdominal terga, thicker than sternal setae (Fig. 84); slightly sclerotized expansion at each side of eighth abdominal tergum; western coastal species .... *macnabeana* Alexander

Setae on abdominal terga 6 and 7 about as thick as those of corresponding sterna, not conspicuously blackened (Fig. 104); eighth abdominal tergum of about uniform length throughout; species of eastern United States .... *scita* Walker

5. Anterior femora slender at base, expanded toward mid-length and thick in apical half (Fig. 168); ninth abdominal sternum interrupted medially, each arm slightly bifurcate at apex and expanded subapically (Fig. 170) .... *carolus* Byers

Anterior femora not conspicuously thickened in apical half; ninth abdominal sternum if interrupted medially (*stoneana, valga*) without apical bifurcation or subapical expansion 6

6. Antennae with 5 or more flagellomeres (4-6 beyond fusion segment) 7

Antennae with 4 or fewer flagellomeres (1-3 beyond fusion segment) 11

7. Cerci long, slender, about 8-9 times their greatest width in lateral aspect 8

Cerci shorter, about 5-6 times their greatest width in lateral aspect 9

8. Hypovalves approximately 2.5-3 times as long (measured from notch to tip) as their greatest width (Fig. 147); mesonotum abruptly downcurved to pronotum (Fig. 140); arms of genital furca thick (Fig. 148); species chiefly of eastern United States and Canada .... *valga* Harris

Hypovalves approximately 4 times as long as their greatest width (Fig. 95); mesonotum not abruptly downcurved to pronotum; arms of genital furca slender (Fig. 96); species of northwestern United States and southwestern Canada .... *nivicola* Doane

9. Cerci obtusely rounded at tip; eighth abdominal tergum expanded at sides (Fig. 125); apex of ninth sternum recurved ventrad (Fig. 126) .... *obtusa*, new species

Cerci acutely tipped; eighth abdominal tergum not expanded at sides, of about uniform length throughout (Figs. 189, 211); apex of ninth sternum a backward-projecting point 10

10. Hypovalves with ventral margin strongly curved upward, dorsal margin nearly straight (Fig. 189); median plate of ninth abdominal sternum not distinctly attached laterally to arms of sternum (Fig. 190) .... *excavata*, new species

Hypovalves with dorsal and ventral margins about equally curved toward apex (Fig. 211); median plate of ninth abdominal sternum clearly attached laterally to arms of sternum (Fig. 212) .... *lyrata*, new species

11. Eighth abdominal tergum expanded at sides to approximately half length of seventh tergum (Fig. 112); antennae usually with single flagellomere beyond fusion segment .... *hybrida*, new species

Eighth abdominal tergum not expanded at sides, much less than half length of seventh tergum throughout; antennae usually with 2 or more flagellomeres beyond fusion segment (rarely only 1) 12

12. Cerci widest beyond mid-length, ventral margin abruptly upturned to apex (Fig. 135); ninth sternum narrowly interrupted medially, its arms nearly converging on dorsal surface of rounded, membranous median lobe (Figs. 134, 136) .... *stoneana* Alexander

Cerci widest near base, narrowing more or less evenly toward apex; ninth sternum sclerotized medially (but see *durbini*, Fig. 180), without membranous median lobe 13

13. Cerci long, slender, 7-9 times their greatest width in lateral aspect, or about twice as long as terga 9-10 together (Figs. 160, 179); hypovalves 3-3.5 times as long as their greatest width 14

Cerci only 4-6 times their greatest width in lateral aspect, or 1.2-1.6 times length of terga 9-10 together (Figs. 189, 199, 216); hypovalves only about twice as long as their greatest width 15

14. Ninth abdominal sternum with a tridentate, darkly sclerotized median plate (Figs. 161, 162); abdominal terga darkened along anterior margin and medially .... *alexandriana* Garrett

Ninth abdominal sternum only lightly sclerotized medially, without posterior teeth (Fig. 180); abdominal terga darkened along posterior margin and medially, with hairs arising from darkly pigmented spots .... *durbini*, new species

15. Median plate of ninth abdominal sternum narrowly triangular, not distinctly attached at sides to arms of sternum (Fig. 190) .... *excavata*, new species

Median plate of ninth abdominal sternum wider than long, distinctly attached at sides to arms of sternum (Figs. 200, 217) 16

16. Median plate of ninth abdominal sternum with 3 low, rounded lobes its central area less darkly sclerotized than outer borders (Fig. 200); cerci flattened, appearing much wider in dorsal aspect than in lateral aspect (Figs. 197, 199); overall body color light brown to brown .... *jellisoni*, new species

Median plate of ninth abdominal sternum with straight posterior margin, or slightly lengthened near mid-line, evenly darkened (Fig. 217); cerci not flattened; overall body color black to dark brown .... *nigra*, new species

The C. scita Group

General body color yellowish, light yellowish brown, or brown; antennae of 8-12 segments (scape, pedicel, fusion segment and 5-9 additional flagellomeres); male gonapophyses blade-like, more or less vertically oriented (compressed), without upturned apical hook; dististyles usually with dorsomesal lobe; eighth abdominal tergum of female short throughout or expanded laterally to more than half length of seventh tergum; cerci and hypovalves long, slender. Included species: *C. albertensis*, *C. macnabeana*, *C. nivicola*, *C. scita*, and *C. wilsoni*, new species.

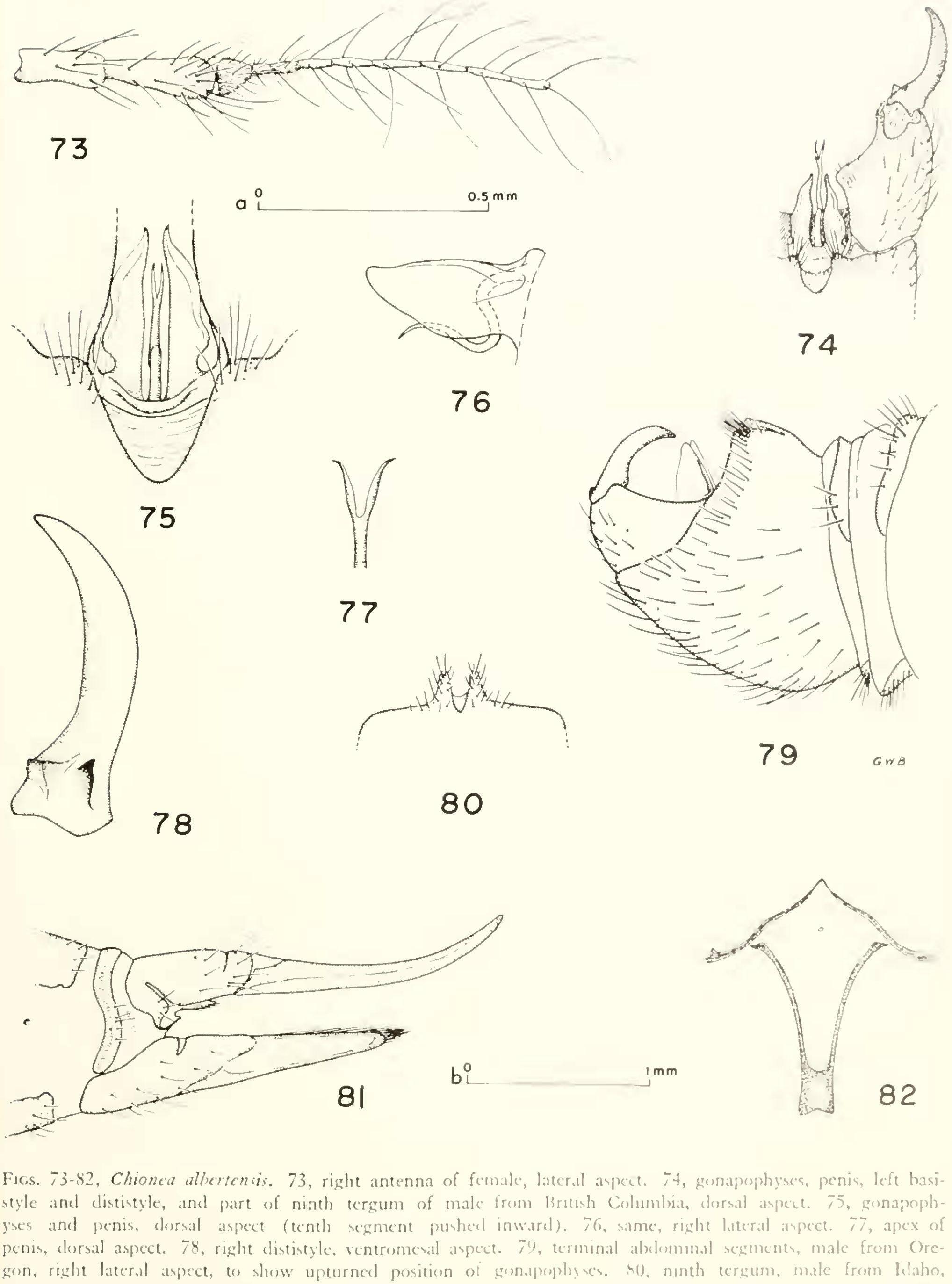
Chionea albertensis Alexander

Chionea albertensis Alexander, 1941: 211-212; Alexander, 1965: 72.

Diagnosis.—A western montane species, yellowish to yellowish brown in color, with antennae of 10-11 segments; male gonapophyses blade-like, acute at apex in dorsal aspect; female cerci very long and slender, ninth sternum acutely pointed at convergence of two narrow bands, each bordering an indistinct, sclerotized area.

Description.—General appearance: Head dark yellowish brown, thorax yellowish brown; legs long, yellowish; abdominal terga dull yellowish brown, slightly darker brown laterally and faintly so along midline; sterna dull yellowish brown; ninth segment of male dark yellowish brown to reddish brown, cerci of female light amber-yellow; pleural membranes pale yellowish brown. Length of male about 5-9 mm, female about 6-7 mm, exclusive of antennae.

Head: Antennae (Fig. 73) consisting of short subcylindrical scape, about three times as long as its diameter, club-shaped pedicel approximately 25% longer than



Figs. 73-82, *Chionea albertensis*. 73, right antenna of female, lateral aspect. 74, gonapophyses, penis, left basistyle and dististyle, and part of ninth tergum of male from British Columbia, dorsal aspect. 75, gonapophyses and penis, dorsal aspect (tenth segment pushed inward). 76, same, right lateral aspect. 77, apex of penis, dorsal aspect. 78, right dististyle, ventromesal aspect. 79, terminal abdominal segments, male from Oregon, right lateral aspect, to show upturned position of gonapophyses. 80, ninth tergum, male from Idaho, dorsal aspect, showing narrow lobes separated by narrow cleft. 81, terminal abdominal segments, female from British Columbia, left lateral aspect. 82, ninth sternum and genital furca, female, ventral aspect. Scales: a—73, 75, 76, 78, 82; b—74, 79-81.

scape, and eight or nine flagellar segments; fusion segment asymmetrically subconical, only a little longer than greatest diameter; first one or two segments beyond it short, subcylindrical, with much shorter hairs than on more distal flagellomeres; other flagellomeres elongate, each bearing an irregularly spaced verticil of three hairs. Vertex dark yellowish brown with brownish or grayish pruinosity and sparse but long black setae, sometimes with an indistinct brownish median stripe or elongate spot. Eyes with about 100-120 ommatidia each.

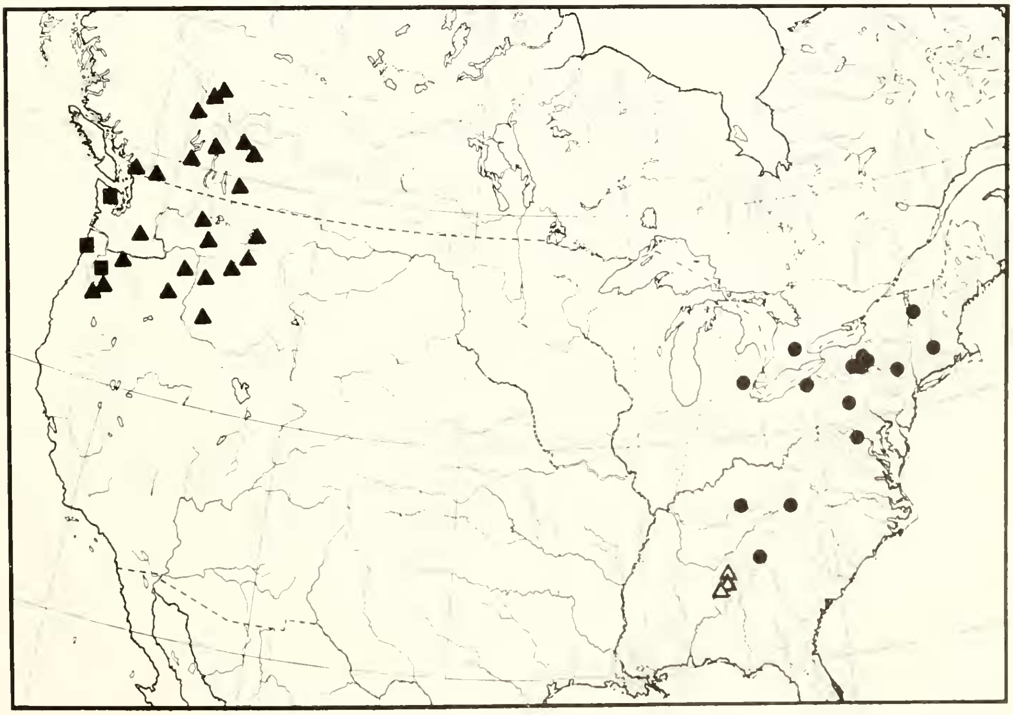
Thorax: Halteres pale dull yellowish brown but not contrasting conspicuously with color of thoracic dorsum. Legs long (hind femora about three-fourths as long as total body length in normally extended specimens), yellowish brown; basitarsi yellowish brown, except brown to dark brown at apex; succeeding tarsomeres brown to blackish brown; claws very long, slender. Setae of legs black, longest on tibiae; usually seven (4 dorsal, 3 ventral) rows of femoral setae, males sometimes with additional small setae not in rows. Approximately 12 long, black setae in each of two poorly defined rows on mesothoracic dorsum; sparse, shorter setae on pronotum and on pleuron above middle coxa; several on each coxa.

Abdomen of male: Posterodorsal edge of ninth tergum (Figs. 74, 80) with a V-shaped to U-shaped median emargination, usually deeper than wide, at each side of which is a small, thick lobe bearing 6-15 dark brown setae. Gonapophyses (Figs. 75, 76) blade-like, thick at base but abruptly compressed to thin, roughly triangular blades, acutely rounded at apex, almost vertically oriented in apical half, ventral edges a little closer together than dorsal edges; space between gonapophyses, seen from above, almost parallel-sided; apex of penis flared outward, produced into two acuminate points (Fig. 77). Basistyles elongate, only moderately thick for genus; posteromesal lobes pilose, simply rounded. Dististyles (Fig. 78) dark yellowish brown, usually smoothly curved and acutely tipped; mesal tooth near base of dististyle prominent, somewhat wedge-shaped with rounded to subacute apical edge, strongly sclerotized; ventral tooth well developed though not projecting conspicuously in most specimens, usually acute and black at tip, less often blunt. Tenth segment pale yellowish gray, not abruptly narrowed near mid-length but broader at base than at apex. Anterior terga bearing long, black setae along caudal margins, smaller setae laterally, sternal setae more slender, not as blackened, longest and most numerous at posterolateral corners.

Abdomen of female: Eighth tergum short (i.e., slender) throughout, yellowish brown, with an indistinct, transverse, reddish brown stripe running its entire width. Hypovalves of eighth sternum long, slender, tapering evenly toward narrowly rounded apex (Fig. 81). Arms of genital furca of about equal thickness throughout, evenly curved outward to attachment with ninth sternum (Fig. 82); basal portion longer than wide, not darkly sclerotized except at lateral margins. Ninth sternum (Fig. 82) formed by two narrow, darkly sclerotized bands converging at an acute point; integument immediately posterior to each band lightly sclerotized except near mid-line; in some females, junction not as strongly or extensively sclerotized as rest of bands. Cerci long, slender, about 8-9 times as long as greatest width, evenly curved both dorsally and ventrally, with acute tips, about 1.4 times as long as hypovalves measured from notch to tip. Sixth and seventh terga with scattered slender, brownish setae; sternal setae sparse.

Types.—Holotype, male, Banff, Alberta, with no additional data. The specimen is damaged, the body broken and only two legs remaining; the genitalia have been cut off and mounted in balsam on a square of celluloid attached to the pin, and although this method of preservation has in many cases proved unsatisfactory, the details of the hypopygium can still be made out readily. The holotype is in the United States National Museum, Washington, D.C. Two legs and one antenna from the holotype are mounted on a microscope slide in the collection of Dr. C. P. Alexander, now in the U.S. National Museum.

Variation.—In some individuals, the apical end of the fusion segment is narrowed to the diameter of the adjoining flagellar segment and may give the appearance of an additional segment. This part may actually become articulated with the fusion segment, producing two similar, short-cylindrical segments without verticils before the rest of the flagellum. In fact, I have seen two males from Cranbrook, British Columbia, in which one antenna has one more flagellomere than the other. Eight segments beyond the fusion segment seems to be the more common condition, occurring in about three-fourths of the specimens examined. The setae of the head, thorax, legs and abdomen, although often long, thick, dark and therefore conspicuous, do not occur in any fixed pattern, and even those on a particular sclerite may vary greatly in size and number from one individual to the next. All parts of the hypopygium of the male are variable, notably the dististyles, which in the holotype are a little shorter, thicker and less evenly curved than in most other males seen. Also, the basistyles in the holotype are shorter and more stout than in an average male of the species. In a male from Clearwater County, Idaho, the lobes of the ninth tergum are prominent, considerably longer than wide, and the median emargination is quite narrow (Fig. 80). This same male is the only one seen lacking the blackened



Map 1. Ranges of *Chionea albertensis* (solid triangles), *C. macnabeana* (squares), *C. scita* (circles) and *C. wilsoni* (open triangles). Each symbol represents one or more collections within a county (in the United States) or at a locality.

ventral tooth on the dististyles. A large, robust male from northeastern Oregon has the basistyles depressed somewhat into the ninth sternum, the gonapophyses correspondingly appearing turned upward (Fig. 79).

Relationships.—Several characters, including body coloration, antennal structure, and form of the ovipositor and ninth sternum of the female, as well as the gonapophyses of the male, point to the relationship of *Chionea albertensis* with *C. macnabeana* Alexander in the western mountains and *C. scita* Walker and *C. wilsoni,* new species, in eastern North America. The female of *albertensis* is smaller than that of *macnabeana* and has fewer antennal segments (10 or 11, as compared to 12 in *macnabeana*) and less conspicuous setae on the posterior abdominal terga. The scape and pedicel of the antenna in *albertensis* are more slender than their counterparts in *macnabeana* and the pedicel longer. Both species appear to have the genital furca of similar shape except for the illustrated difference in curvature of the arms, which may be an artifact of preservation. Differentiation of males of *albertensis* from those of *scita* is an easy matter. The obvious character is the ninth tergum, emarginate medially, with setiferous lobes bordering the emargination in *albertensis*, but entire (very broadly indented in posterodorsal aspect) in *scita*. The apex of the penis in *albertensis* is bifurcate with two slender points, but in *scita* it is somewhat spoon-like. The surface of the gonapophyses in males of *albertensis* is more undulating and the apex more acute than in *scita*. Ordinarily, also, the number of antennal segments in *albertensis* is one less than in *scita*, and *scita* does not appear to be as long-legged as *albertensis*. These last named characters apply to females as well as males. Females of *albertensis* may be distinguished from those of *scita* also by the ninth sternum and the number of antennal segments, and in *albertensis* the bursa copulatrix is long and curved, not looped as in *scita*.

The recently discovered male of *C. macnabeana* agrees with the relationships described on the basis of the females.

Geographic Distribution.—Present collection records show that *Chionea albertensis* occurs from mountainous eastern British Columbia and western Alberta southeastward along the Bitterroot Range and nearby mountains into Idaho and western Montana, also southward to northeastern Oregon and westward to southwestern British Columbia (Map 1).

Seasonal Distribution.—Although most specimens have been taken in November, there are records for late August, mid-October, January, February, and mid-March, the last in Cranbrook, British Columbia, the only locality in which several individuals have been collected. I anticipate that further and especially concentrated local collecting will yield a clear picture of two generations a year.

Habitats.—About all that can be said of the habitats of *albertensis* is that it occurs in forested, generally mountainous areas within the described geographic range. Even this comes only from my own observations of the collecting areas, made primarily in summer. As far as I am aware, all known specimens were taken on the surface of snow; unfortunately, detailed ecological data are available for only a few of them.

Collection Records.—ALBERTA: Banff, no other data (holotype); Banff National Park, Boulder Pass, 7490 ft, on 12 in of snow, 14 Oct. 1968, K. W. Richards (1 ♀); Jasper National Park, 7600 ft, 18 Aug.-1 Sept. 1970, P. Kuchar (1 ♂, 1 ♀). BRITISH COLUMBIA: Cranbrook (49° 31′N, 115°46′W), elevation about 3000 ft, on snow, 16 March (1 ♂), 1 Nov. (1 ♀), 2 Nov. (1 ♂), 4 Nov. (1 ♂, 2 ♀), 15 Nov. (1 ♂, 2 ♀), all collected by C. B. D. Garrett, no years recorded; Goldstream River, 52°45′N, 118°45′W, 26 Dec. 1979, J. G.

Woods (6♂, 5♀); Mt. Revelstoke National Park, 28 Dec. 1976, J. G. Woods (1♀); Wells Gray Provincial Park (about 50°30′N, 120°00′W), along willow flats, Stillwater, 1 Jan. 1962, P. Joslin (1♂); Manning Prov. Park, Lightning Creek, on snow at dusk, about 0°C, 4000 ft, 9 Feb. 1980, R. J. Cannings (1♀); same but Similkameen River, 4000 ft, 11 Feb. 1978, S. G. Cannings (1♀); same but Chowanten Creek, about 0°C, overcast, 4000 ft, 17 Feb. 1980 (1♀); Vancouver, Hollyburn Mountain, 16 Feb. 1980, L. Vasington (1♀); Silver Star Mt. (15 mi NE of Vernon), light snow, −3°C, 29 Jan. 1981, A. Bryan (1♀). IDAHO: Benewah Co., Crystal Creek, on snow, 22 Dec. 1968, M. M. Furniss (1♂); Boise Co., 11 mi N of Idaho City, on snow in pine forest, 30 Nov. 1974, G. A. Shook (1♂); Clearwater Co., 8 mi N of Elk River, 19 Nov. 1961, E. H. Dustman (1♂); Clearwater Co., E Fork of Potlatch River, 5.5 mi E of Bovill, on snow, 11 Dec. 1978, R. C. Biggam, T. F. Hansen and P. C. Schroeder (1♂, 2♀); Idaho Co., Clearwater National Forest, Mud Creek Jct., 25 Nov. 1978, R. C. Biggam and M. A. Maurer (1♂, 1♀); Idaho Co., Warm Springs Creek, about 20 mi SW of Lolo Pass on U.S. Hwy. 12, 28 Dec. 1975, A. Greene (2♀). MONTANA: Lake Co., vicinity of Univ. of Montana Biological Station, from oil-formalin-alcohol traps, in snow, 24 Dec. 1972 (2♂, 5♀), 6 Jan. 1973 (2♂, 3♀), 21 Jan. 1973 (2♂, 1♀), 23 Jan. 1973 (1♀), 12 Feb. 1973 (2♂), 17 Feb. 1973 (2♂, 3♀), all collected by D. S. Potter; Missoula Co., Lolo vicinity, Bitterroot Mountains, about 6000 ft, on fresh snow, Nov. 1950, J. A. Chapman (1♂); Missoula Co., Elk Creek, Lubrecht Forest, 4000 ft, 22 Jan. 1972, R. A. Haick (2♀); Grant Creek, GC-3, 13 Feb. 1972, R. A. Haick (2♂). OREGON: Grant Co., Anthony Lakes Ski Area, on snow, 18 Feb. 1974, K. Goeden (1♂); Lane Co., Pengra Pass, 5100 ft, 22 mi SE of Oakridge, 4 Jan. 1975, J. Lattin (1♂); Linn Co., Santiam Pass, 2 mi N of Santiam Hwy., 2:30 p.m., on snow, 30 Dec. 1977, J. D. Lattin (1♀); Wallowa Co., Wallowa-Whitman National Forest, Eagle Cap Wilderness Area, 6000-7000 ft, weather clear, 24 Nov. 1972, A. Greene (1♂); Wasco Co., 15 mi SE of Government Camp, Frog Lake Butte, 31 Dec. 1975, P. J. Johnson (1♂, 1♀). WASHINGTON: Spokane Co., Mt. Spokane State Park, 5000 ft, 9 Nov. 1975, A. Greene (1♂); Yakima Co., 5-6 mi E of Chinook Pass, on snow about 2.5 ft deep, 17 Dec. 1977, P. J. Johnson (1♀); 15 mi E of Chinook Pass, on snow about 2.5 ft deep, 17 Dec. 1977, P. J. Johnson (1♂); Yakima Co., Sand Lake, 2 mi N of White Pass, Snoqualmie National Forest, 5295 ft, walking on snow 30-45 cm deep, in coniferous forest, 25 Nov. 1979, W. Kaltenthaler (1♂).

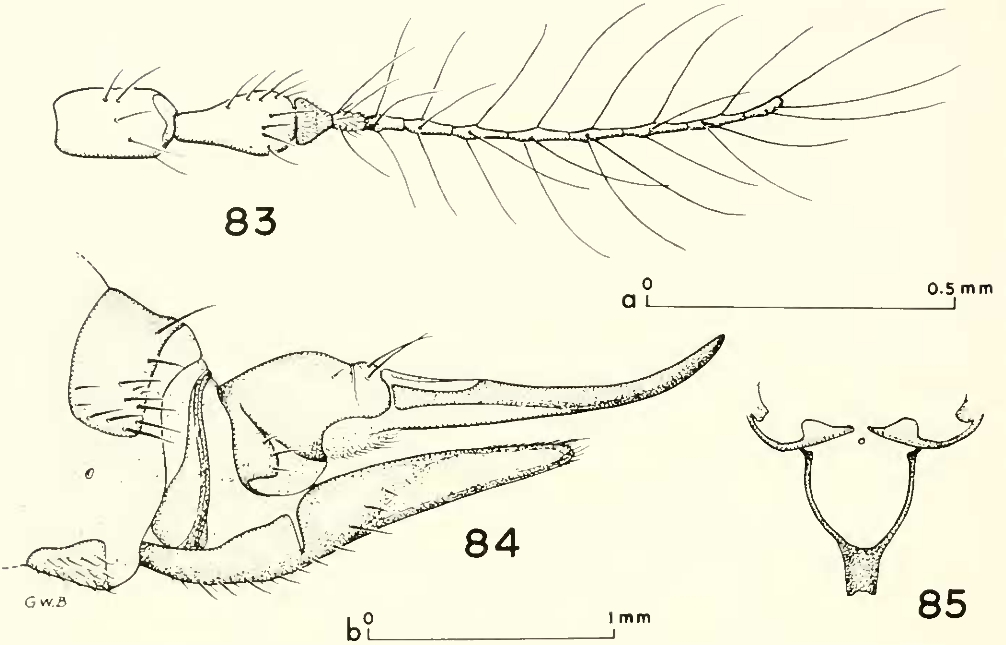
Chionea macnabeana Alexander

Chionea macnabeana Alexander, 1946: 156; Alexander, 1954: 69; Alexander, 1965: 72.

Diagnosis.—A large west coast species of yellowish brown color, with antennae of 12 segments, scape and pedicel thick; female cerci very long and slender; sixth and seventh abdominal terga bearing several thick, blackened spines, especially on posterolateral corners; male gonapophyses appearing broadly rounded with inner apical point, in dorsal aspect.

Description.—General appearance: Head, thorax, legs and abdomen yellowish brown to light brown, head slightly darker than thorax; sclerites not much darker than membranous areas; cerci of female long, amber colored, palest at base. Length of female, exclusive of antennae, about 8.2-9.4 mm.

Head: Antennae (Fig. 83) consisting of thick, subcylindrical scape, short, club-shaped pedicel, and ten flagellomeres; fusion segment short-conical, or turbinate, shorter than its basal diameter, partially



FIGS. 83-85, *Chionea macnabeana*. 83, antenna of female holotype (from slide in C. P. Alexander collection). 84, terminal abdominal segments, female from Washington, left lateral aspect. 85, ninth sternum and genital furca, female, ventral aspect. Scales: a—83, 85; b—84.

subdivided in one specimen seen; first flagellomere beyond it short, cylindrical, bearing many short, fine hairs in addition to verticil of three hairs which are shorter than those of succeeding flagellomeres. Antennal length about 1.5 mm. Setae of vertex stout, long, black. Eyes with about 200 ommatidia each.

Thorax: Halteres tan, not contrasting conspicuously with color of thoracic dorsum. Legs slender (femora not incrassate), yellowish brown, tarsi only a little darker brown. Setae of legs long, stout, black; those in dorsal rows slightly larger and thicker than ventral setae. Setae of coxae, thoracic dorsum, and sternal sclerites stout, black.

Abdomen of male: See Appendix 2.

Abdomen of female: Eighth tergum short (i.e., slender) dorsally with lightly sclerotized anterior expansion at each side (Fig. 84), posterior margin more darkly sclerotized. Hypovalves of eighth sternum long, slender, evenly tapered toward narrowly rounded apex. Ninth tergum with three short setae near posterolateral margin on each side; tenth tergum mostly bare with two setae on each side near posterior margin. Tenth tergum somewhat humped upward near mid-length, and anteriorly its sides extended and curved ventrad. Arms of genital furca of approximately uniform thickness throughout, smoothly curved outward to points of attachment on ninth sternum; basal portion a little longer than wide, most strongly sclerotized at sides. Ninth sternum (Fig. 85) formed by two slender, well sclerotized bands with expanded tips which almost meet medially. Cerci long, slender, about eight times as long as greatest width, evenly curved both dorsally and ventrally to acute tips, noticeably longer than hypovalves (about 1.17 times as long as hypovalves measured from notch to tip). Sixth and seventh terga with thick, blackened setae along posterolateral margins, most conspicuous on seventh tergum; sternal setae blackened but generally shorter and more slender than those on dorsum.

Types.—Holotype, female, Wilson River, Tillamook Co., Oregon, elevation 2125 ft, 8 February 1946, James A. Macnab collector. The type is mounted on a microscope slide in the collection of C. P. Alexander, Amherst, Massachusetts (transferred in 1981 to the U.S. National Museum, Washington, D.C.).

Relationships.—That *Chionea macnabeana* belongs to the *scita* group is indicated by the pale body, the relatively large number of antennal segments, and the similarity in structure of the female genital segments between this species and *C. albertensis* and particularly *C. scita.* A discussion of the relationships of *macnabeana* and *albertensis* will be found under the heading of the latter species. The most useful differences for separating these two western species are the greater number of flagellomeres and shorter, thicker scape and pedicel in *macnabeana* and the presence of thick, black setae on the sixth and seventh abdominal terga, where in females of *albertensis* the setae are more slender, not as darkly colored, and more sparsely distributed. Females of *macnabeana* and *scita*, both of which may have 12 antennal segments, may be differentiated by the detailed structure of the genital furca and ninth sternum. The furca in *scita* is somewhat more lyriform and the ninth sternum interrupted at the mid-line, with a longitudinal bar at each side of the break (Fig. 94). Also, as pointed out by Alexander (1946: 156, as *primitiva*), females of *scita* are on the average smaller, with "more delicate vestiture" on the legs.

Geographic Distribution.—For 25 years this species was known only from the type locality in northwestern Oregon. The second known specimen was collected 30 December 1971, about a mile east of the eastern end of Lake Crescent, Clallam Co., Olympic Peninsula, Washington, between 900 and 1300 ft (277-400 m), by N. D. Penny. Both these localities are low on the outer slopes of the northern Coast Ranges (Map 1). Both are in somewhat isolated mountainous regions separated from the higher Cascade Range by the Willamette Valley in Oregon and by Puget Sound in Washington. The species may occur northward into British Columbia and almost surely southward in Oregon. One male was recently collected on snow at 5200-5500 ft, in the Sentinel Hills, Mt. Jefferson Wilderness, Linn Co., Oregon, on 22 March 1981, by Dr. L. K. Russell.

Seasonal Distribution.—The holotype of *macnabeana* was collected in early February, which is about mid-season for the appearance of western Chioneas generally. However, the specimen was taken at a lower elevation than most, which probably relates to its seasonal occurrence, the arrival of winter weather being later there.

Habitats.—The type locality is the "Tillamook burn," a forested area which was swept by fire in 1933, 1939, and again in 1945, only a few months before the specimen of *Chionea macnabeana* was collected. The fly was found on snow about 20 in deep, during a snow storm. The female from the Olympic Peninsula was also found on snow.

Chionea nivicola Doane

Chionea nivicola Doane, 1900: 188-189; Alexander, 1949: 319; Alexander, 1965: 72.

Diagnosis.—A western species with brown coloration, antennae of eight or nine segments (6 or 7 flagellomeres); male gonapophyses blade-like, approximately vertically oriented, female cerci slender, slightly upturned in apical half.

Description.—General appearance: Head dark brown, thorax light brown dorsally, brown at sides; abdominal sclerites light brown to brown, except ninth segment of male darker brown, cerci of female amber colored; pleural membranes pale grayish brown. Length of male about

5 mm, female about 4-8 mm, exclusive of antennae.

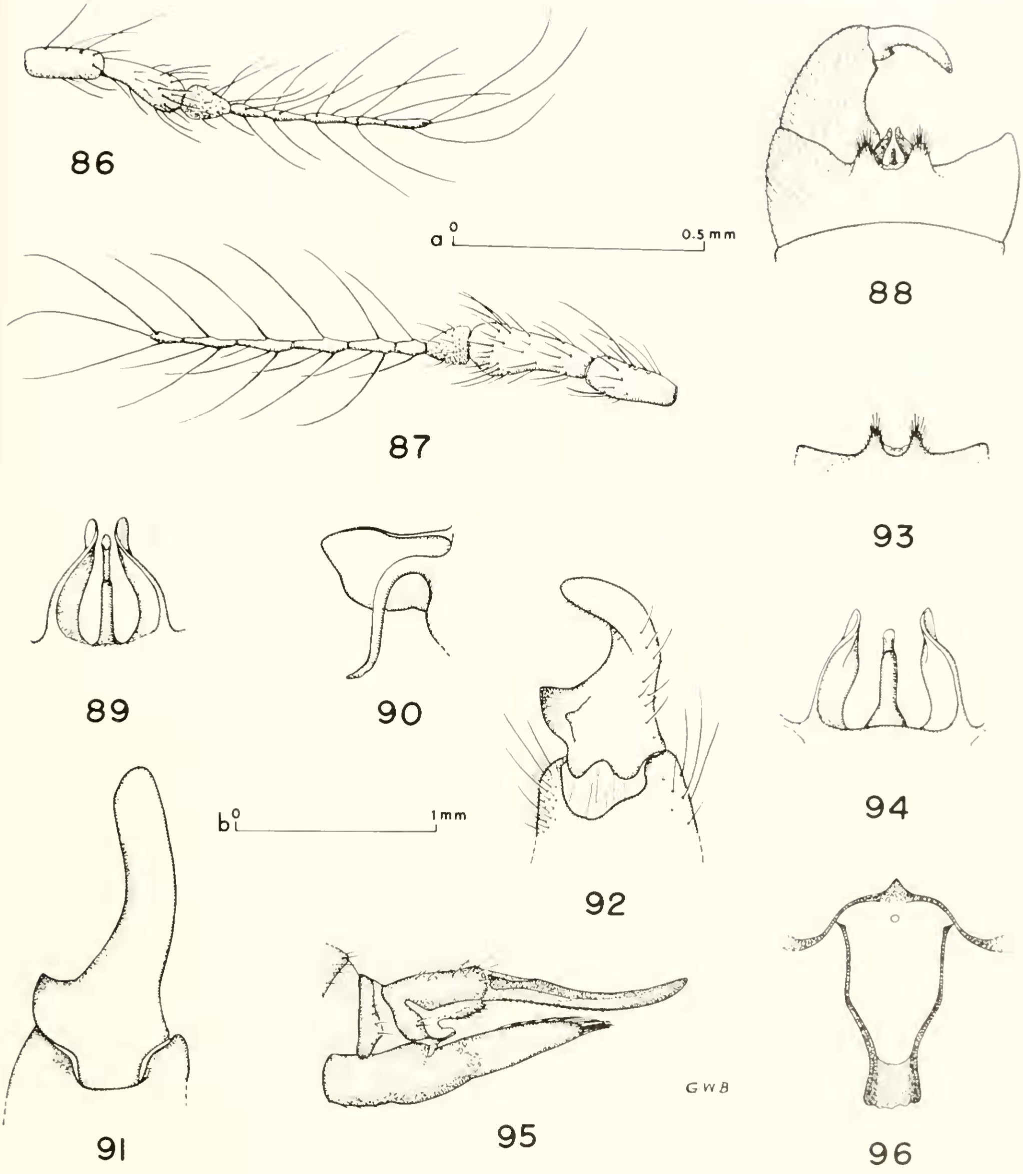
Head: Antennae (Figs. 86, 87) comprising scape, pedicel and six or seven flagellomeres; fusion segment asymmetrically short-conical, about as long as greatest diameter, with apical portion sometimes resembling additional segment. Setae on vertex short, curved, stout. Eyes with about 80-100 ommatidia each.

Thorax: Color of thoracic dorsum light brown to dark yellowish brown centrally, darkening to brown laterally on pronotum and on posterior metanotum; pale grayish brown spot on dorsal mid-line of metanotum in some individuals. Halteres pale grayish brown, contrasting somewhat with color of thoracic dorsum. Mesonotal setae sparse, short, stout, often in transverse patch interrupted at mid-line. Legs long, hind femora extending far beyond end of abdomen, femora light brown, with seven (4 dorsal, 3 ventral) longitudinal rows of short, curved thick and darkened setae; tibial setae longer, more slender. Tarsomeres beyond basitarsi darkening to brown, dark brown on last two.

Abdomen of male: Setae on terga very short, sparse, occurring mostly along posterior and lateral margins. Sternal setae mostly short, on posterior margins, longer and more dense on posterolateral corners of fifth through seventh sterna and on posterior edge of eighth sternum. Posterodorsal margin of ninth tergum (Fig. 88) bearing two prominent, setiferous lobes; median space between these projections broadly U-shaped; 6-11 straight, thick setae on each lobe. Gonapophyses seen from above (Fig. 89) blade-like, almost vertically oriented, curved outward laterally, concave on mesal surfaces with bluntly rounded tips almost touching dorsally, curving apart ventrally; space between gonapophyses broadest basally, usually narrow posteriorly; apex of penis flattened and slightly expanded. Basistyles elongate, slender for genus, sometimes paler than ninth sternum; posteromesal lobes inconspicuous, pilose, evenly rounded. Dististyles (Figs. 91, 92) dark yellowish brown, broad at base, bowed slightly laterad, then more or less evenly curved to acutely rounded apex; mesal tooth near base prominent, subacute; ventral tooth absent in all specimens seen, but small dorsomesal tooth in a few individuals (Fig. 92, cf. *C. scita*). Tenth segment broad at base, evenly narrowed, pigmented and lightly sclerotized laterally.

Abdomen of female: Tergal and sternal setae more numerous and more evenly distributed over sclerites than in males. Eighth tergum at sides about half as long as seventh, shorter dorsally, with three to five posterolateral setae. Hypovalves of eighth sternum slender, elongate, with upper margin gradually and evenly curved downward, lower margin straight for most of its length, then curved upward to tip (Fig. 95). Arms of genital furca tapering rather evenly from base to tip, more strongly divergent in basal half than in apical half, with noticeable bend near mid-length (Fig. 96); basal portion wider than long, not densely sclerotized medially; entire structure lyriform. Mid-ventral portion of ninth sternum (Fig. 96) lightly sclerotized, produced caudad as short, acute or subacute point. Cerci elongate, slender, about eight to nine times as long as greatest width, slightly curved upward in apical half, in some specimens widened beyond mid-length, noticeably longer than hypovalves (about 1.3-1.4 times as long as hypovalve measured from notch to tip; Fig. 95).

Types.—Four female syntypes, Pullman (Whitman Co.), Washington, published without further data. I have seen three of these, which are now in the United States National Museum, Washington, D.C. Two (pinned) are labelled Pullman, Washington, on snow, R. W. Doane collector, and dated 9 January and 12 January 1899; both have been given U.S.N.M. catalogue number 7025. The third I have



Figs. 86-96, *Chionea nivicola*. 86, right antenna of pinned female, lateral aspect. 87, right antenna, female from Oregon, in fluid, mesal aspect, showing six flagellomeres beyond fusion segment. 88, ninth abdominal segment of male from Washington, dorsal aspect (left basistyle and dististyle omitted). 89, typical gonapophyses and penis, dorsal aspect. 90, left gonapophysis and penis, right lateral aspect; cf. Fig. 94. 91, right dististyle, ventral aspect. 92, left dististyle, dorsomesal aspect. 93, posterior margin of ninth tergum, small male from Idaho, dorsal aspect. 94, atypically widely separated gonapophyses, dorsal aspect (same male as Fig. 90). 95, terminal abdominal segments, female syntype (USNM), left lateral aspect. 96, ninth sternum and genital furca, female, ventral aspect. Scales: a—86-87, 89-92, 94, 96; b—88, 93, 95.

cleared and mounted on a microscope slide. It was labelled "*Chionea*—on snow, 12-5-99." The remaining syntype is in the collection of Washington State Univ., Pullman.

Variation.—Among the specimens examined, about half have five flagellomeres beyond the fusion segment, the others six, with the first being shortest (Fig. 87). Some individuals have a dark brown median longitudinal stripe on the vertex and occiput. One female was seen in which the halteres contrasted conspicuously with the thoracic dorsum by reason of its unusually dark color. The cerci of some females are slightly but noticeably widened in the apical half, which increases the curvature of the ventral margin and gives the cerci the appearance of being more abruptly upturned. In a few of the larger, more robust males, the basistyles are thicker than illustrated, but the ventral tooth of the dististyle is not developed as it is in robust males of some other species in which it is more often absent. Although the tips of the gonapophyses are usually strongly convergent (Figs. 88, 89) and rarely are seen in contact, they may be widely separated (Fig. 94). The penis is ordinarily more upcurved apically than as shown in Figure 90. Occasional presence of a small tooth on the inner surface of the dististyle and more dorsal than the large mesal tooth (Fig. 92) has been mentioned in the description.

Size variation, as usual for the genus, is striking. In a population from Latah Co., Idaho (Moscow Mountain), sampled on 9 December 1971, the shortest male was only .67 times as long as the largest male, and its hind femur was only .53 times as long as that of the largest male. Although the basistyles of the smaller males were considerably more slender in lateral aspect than those of more robust males, their length—probably of more functional importance in grasping the female—was in a ratio of about .82 to 1. Other genitalial measurements also showed less size variation: width of ninth tergum .76 to 1, length of dististyle 1 to 1, length of gonapophyses approximately 1 to 1.

Certain parts of the original description, notably the references to concave areas on the femora and tibiae and to the abdomen's being only six-segmented, are somewhat misleading and are based upon Doane's observation of dried, rather shriveled specimens.

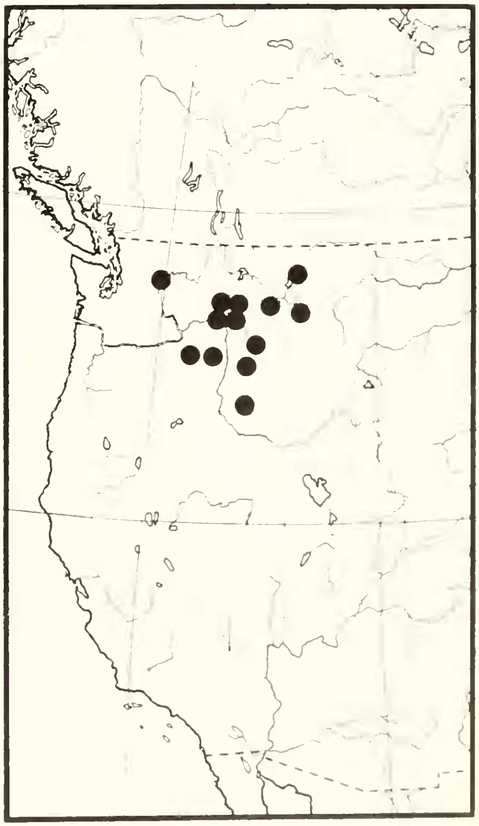
Relationships.—While antennal structure, the eighth abdominal tergum of the female and perhaps body color suggest *C. nivicola* belongs with the *valga* group, the form of the male gonapophyses does not support this placement. The gonapophyses are in fact most like those of *C. albertensis.* The long, slender cerci and hypovalves of the female also resemble those of females in the *scita* group. Presence of a prominent mesal tooth and occasional dorsomesal tooth at the base of the dististyle is similar to the condition seen in *C. scita.* The long and, even in males, not greatly thickened femora in *nivicola* resemble those of *albertensis.* Within the *scita* group *nivicola* is easily recognized by its body color and number of antennomeres. In the field it may occur together with *albertensis* but also frequently with *alexandriana* and *obtusa,* which it resembles in general coloration. From these it may readily be differentiated by having longer antennae than *alexandriana* (6 or 7 flagellomeres in *nivicola,* only 3 or 4 in *alexandriana*) and tergal lobes (♂), slender cerci (♀) and short femoral setae, contrasted with absence of tergal lobes, short, thick cerci and conspicuously long femoral setae in *obtusa.* The short, thick setae of head, thoracic dorsum, abdomen and legs are found elsewhere among North American species only in *C. stoneana.*

Geographic Distribution.—As now known, the range of *C. nivicola* includes the Columbia Basin and the mountains surrounding it: the eastern Cascade Range to the west, the Blue Mountains to the south, and the Salmon Mountains, Clearwater Mountains and Bitterroot Range to the east and northeast, but also over the last of these to the western slopes of the Rocky Mountains in Montana (Map 2). I expect the species may range into southwestern Canada and perhaps may occur in the eastern Cascade Range of Oregon.

Seasonal Distribution.—Records for mid-November are from mountainous areas at higher elevations than the Washington and Idaho localities at which *C. nivicola* was taken in December and January. This seems to conform to the general pattern of earlier appearance of *Chionea* in areas where cold winter sets in first and subsequent appearance at lower latitudes or elevations. This pattern of seasonal distribution suggests a second generation of *nivicola* may occur in March and April in the colder parts of the range.

Habitats.—Most specimens were found on snow, in areas of fairly open forest, at elevations from about 740 to 1850 m, or 2400 ft (type locality) to 6000 ft or more (Oregon). The Oregon specimens taken beneath a log may well have been in an excavation made by a small mammal. There have been too few observations or collections made to justify any other generalizations about the habitats.

Collection Records.—IDAHO: Benewah Co., Crystal Creek, on snow, 22 Dec. 1968, M. Furniss (1 ♂, 2 ♀); Boise Co., Idaho City, 14 Dec. 1974, G. A. Shook (1 ♀); Clearwater Co., 8 mi N of Elk River, 14 Nov. 1961, E. H. Dustman (1 ♂); Idaho Co., Clearwater National Forest, Mud Creek Jct., 25 Nov. 1978, R. C. Biggam and M. A. Maurer (1 ♂, 1 ♀); Mud Creek, Lolo Creek Canyon, 14 Nov. 1975, R. C. Biggam (1 ♂); Latah Co., Moscow Mountain, 9 Dec. 1971, G. W. Urich (10 ♂, 6 ♀); 3 mi S of Helmer, Little Boulder Camp, 4 Dec. 1971, W. J. Turner (1 ♂, 2 ♀); 8 mi E of Moscow, Robinson Lake Road, 6 Dec. 1972, Dunn and Michta (3 ♂, 3 ♀); Big Meadows Rec. Area, 4.5 mi NNW of Troy, 9 Dec. 1973, M. C. Hunter (2 ♀); Moscow, on snow, 8 Dec. 1961, R. E. Stecker (5 ♂, 4 ♀); Latah Co., on snow, 14 Dec. 1960, W. F. Barr (2 ♂, 7 ♀). MONTANA: Flathead Co., Big Fork, 12 Nov. 1973, R. A. Haick (2 ♀); Mineral Co., St. Regis, on snow, 28 Dec. 1957, H. R. Dodge (1 ♂); Missoula Co., Missoula, on fresh snow, about 32°F, 16 Nov. 1952, J. A. Chapman (1 ♀). OREGON: Umatilla Co. (southeast), Bowman Meadows to Fly Creek, on snow, 16 Nov. 1962, J. Schuh and E. Hansen (1 ♂, 3 ♀); Fly Creek valley, under log, 15 Nov. 1961, J. Schuh (1 ♂, 1 ♀); Wallowa Co., Wallowa-Whitman National Forest, Eagle Cap Wilderness, 6000-7000 ft, weather clear, 24 Nov. 1972, A. Greene (1 ♀). WASHING-



Map 2. Range of *Chionea nivicola*. Each spot represents one or more collections within a county.

TON: Chelan Co., Stevens Pass, near 4100 ft, 17 Feb. 1973 (1 ♀); Garfield Co., Saddle Butte, Blue Mountains, 9 Nov. 1970, J. Eves and R. D. Akre (3♂, 2♀); Whitman Co., Pullman, 5 Dec. 1899 (1 ♀), 9 Jan. 1899 (1 ♀), 12 Jan. 1899 (1 ♀), all collected by R. W. Doane (types); Pullman, 15 and 16 Dec. 1970, W. J. Turner (1 ♂, 2 ♀); 7 mi NW of Colton, 21 Nov. 1973, L. Richards (1 ♂).

Chionea scita Walker

Chionea scita Walker, 1848: 82-83; Byers, 1963: 160; Alexander, 1965: 72.

Chionea primitiva Alexander, 1917: 204-205, Figs. 1, 4; Alexander, 1919: 805, 903; Leonard, 1928: 694; Alexander 1942: 428-429.

Diagnosis.—A northeastern species having yellowish brown color, antennae of 12 (rarely 11 or 13) segments, male gonapophyses blade-like, vertically oriented, ninth abdominal tergum entire, without projecting lobes; female cerci evenly curved, not greatly elongated; hypovalves long with nearly straight ventral margins.

Description.—General appearance: Head dark yellowish brown to light brown, thorax yellowish brown; abdominal sclerites yellowish brown faintly mottled with brown; ninth segment of male dark yellowish brown, cerci of female light amber colored; pleural membranes dull, sordid yellowish brown. Length of male about 5-8 mm, female about 6-8 mm, exclusive of antennae.

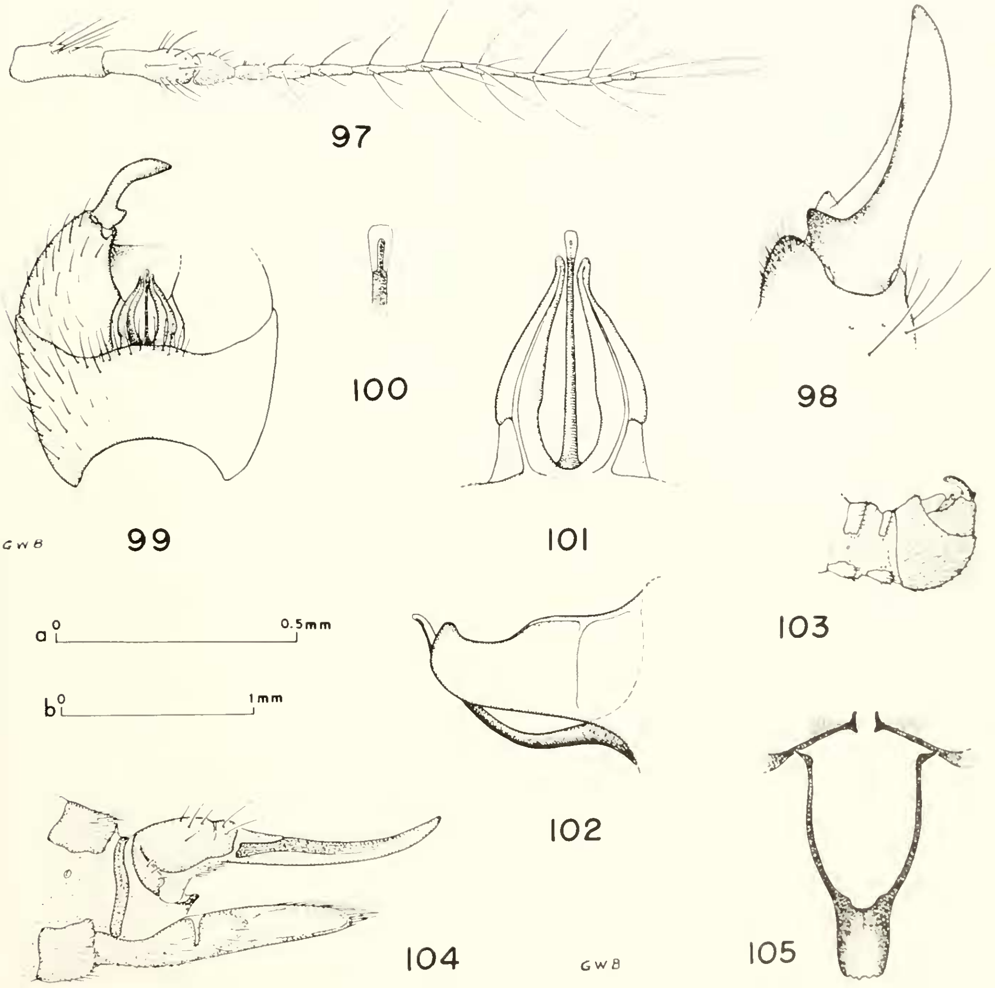
Head: Antennae (Fig. 97) comprising scape, pedicel and usually ten flagellomeres, rarely only nine or as many as 11; fusion segment elongate, conical, longer than its basal diameter, covered with short, fine hairs; second flagellomere also covered with short hairs, third and succeeding segments verticillate, with three, sometimes four, setae. Eyes with about 180-200 ommatidia each.

Thorax: Halteres dull, pale yellowish brown, not contrasting sharply with color of thoracic dorsum. Femora, tibiae and proximal three-fourths of basitarsi yellowish brown, tarsi otherwise dark brown. Femoral setae arranged in four dorsal, three ventral rows, smaller hairs sometimes not aligned with setae. Mesonotal setae long, erect, conspicuous.

Abdomen of male: Posterodorsal margin of ninth tergum (Fig. 99) entire, without projecting lobes, broadly and evenly rounded, arched upward and projecting slightly caudad (appearing broadly emarginate when seen in posterodorsal aspect), bearing about a dozen marginal setae sometimes in two weakly defined groups. Gonapophyses (Figs. 101, 102) slenderly triangular in dorsal profile, with thickened dorsal margins, apices turned slightly inward; form in lateral aspect blade-like (Fig. 92), lower margin curving smoothly upward to meet irregular dorsal margin at upturned, narrowly rounded apex; space between gonapophyses narrow, rounded basally, slightly constricted near base; penis evenly curved, its membranous apex spatulate, with slender ventral sclerotized reinforcement (Fig. 100). Basistyles thick, their posteromesal lobes pilose, simply rounded. Dististyles (Fig. 98) evenly curved beyond base, yellowish brown, with strongly sclerotized, blackened mesal tooth, from which a darkened ridge extends along inner, lower surface of dististyle toward tip, in most specimens; dorsomesal tooth low, blunt, rarely rudimentary or absent. Tenth segment as broad basally as space between basistyles, narrowed evenly toward apex, lightly sclerotized and pubescent on lower, outer surfaces (pushed into ninth segment and not shown in Fig. 99).

Abdomen of female: Eighth tergum short (i.e., slender) throughout (Fig. 104), most densely sclerotized along anterior margin, with narrow, yellowish posterolateral edges. Hypovalves of eighth sternum elongate, slender, tapered toward narrowly rounded apex, lower margins more or less straight, upper margins curving slightly downward. Arms of genital furca divergent from basal plate, then subparallel for about half their length until apically curved outward to join ninth sternum (Fig. 105); basal plate not densely sclerotized medially except for narrow, transverse bar connecting arms. Ninth sternum formed by two converging, slender, well sclerotized bands which arch upward and backward, ending in small longitudinal bars, parallel and separated by a narrow, clear zone at mid-line (Fig. 105); a lightly sclerotized area with rounded margin above terminal portion of each band of sternum. Cerci elongate, about seven to eight times as long as greatest width, noticeably longer than hypovalves (about 1.20-1.36 times as long as hypovalves measured from notch to tip).

Types.—Holotype, female, labelled "North America" but without further



Figs. 97-105, *Chionea scita.* 97, left antenna, male holotype of *C. primitiva,* mesal aspect; length 1.55 mm. 98, right dististyle, ventromesal aspect. 99, ninth abdominal segment of male from Michigan, dorsal aspect (left basistyle and dististyle omitted). 100, apex of penis, dorsal aspect. 101, gonapophyses and penis, dorsal aspect. 102, same, right lateral aspect. 103, terminal abdominal segments, male, left lateral aspect. 104, terminal abdominal segments, female, left lateral aspect. 105, ninth sternum and genital furca, female, ventral aspect. Scales: a—97-98, 101-102, 105; b—99, 104.

data. The type was originally in the British Museum (Natural History) but has been lost sometime since 1953. In that year I sent sketches of diagnostic features of females of *Chionea valga* and what I then called *C. primitiva* to Dr. Paul Freeman, Curator of Diptera in the British Museum. He compared my sketches with the type and confirmed that *primitiva* is the same as *scita*. Subsequently, however, the holotype of *scita* became misplaced, and neither Dr. Freeman nor I was able to locate it when we searched briefly in 1955 and again more thoroughly in 1960. The holotype of *C. primitiva* Alexander is a male from Cascade, Owasco Lake, Cayuga Co., New York, collected on 15 November 1915 by Bishop and Crosby. It is mounted on a microscope slide in the collection of Dr. C. P. Alexander, Amherst, Massachusetts (transferred in 1981 to the U.S. National Museum, Washington, D.C.).

Variation.—Among the many specimens examined, only two had eight flagellomeres beyond the fusion segment, and only one had ten; thus, it can be said that the total number of antennal segments is ordinarily 12. Walker described *scita* as having antennae with black flagella. Since, at the time Dr. Freeman compared the holotype with my drawings, both its flagella were missing, I cannot explain this except to surmise that Walker had viewed the specimen against a pale or illuminated background. The description of the ninth abdominal tergum of the male, above, pertains to the dorsal aspect; because the tergum is somewhat arched upward, it may appear broadly emarginate in posterodorsal aspect. The ventral tooth at the base of the dististyle, which is absent or minute and not darkly colored in some species and even in some males of *scita*, is usually both enlarged and darkly sclerotized. The "tuft of stout black hairs" referred to in the original description of *C. primitiva* (Alexander, 1917: 205) is a group of short, inconspicuous hairs on the mesal face of the dististyle, near the base, occurring in this and all other species. Alexander also described the legs as having all the femora enlarged, which is true of males but not females. Variation in the female cerci and hypovalves has been noted above. In most females the pleura of the tenth abdominal segment hang down at each side in a fleshy, semicircular fold, partially concealing the ninth sternum in lateral view. These folds are more prominent in *scita* than in most other species (Fig. 104).

The specific name is derived from Latin *scita*, meaning beautiful or handsome.

Relationships.—This species is one of four in North America that have yellowish brown overall coloration, antennae with more than nine segments, the eighth abdominal tergum of the female short, and the male gonapophyses blade-like and more or less vertically oriented. These species, together with *nivicola*, comprise the *scita* group. Within this group, *Chionea scita* is set somewhat apart from the other three yellowish species, *C. albertensis*, *C. macnabeana* and *C. wilsoni*, on the basis of such characters of the female as the ninth sternum, the furca and the setae on the abdominal sclerites. Both *scita* and *macnabeana* have 12 antennal segments, as compared to 11 in *albertensis*, but in view of the known individual variation in this character and the fact that *macnabeana* is based upon so few specimens, I would place more reliance in the genitalial characters as indicators of relationship. Males of *scita* differ from those of *albertensis* in having the ninth abdominal tergum entire instead of bilobed, the penis spatulate at the tip instead of forked, the surface of the gonapophyses less undulating than in *albertensis* and the tips less acute. In *scita* there is usually a darkened ridge extending distad from the darkened mesal tooth of the dististyle, while in *albertensis* this tooth is ordinarily not conspicuously blackened, and if a ridge extends distad from it, the ridge is not blackened. Moreover, *scita* lacks the darkly sclerotized ventral tooth seen in *albertensis*. Some other, less outstanding differences will be found in the discussion of the relationships of *C. albertensis*.

Geographic Distribution.—As now known, the range of *Chionea scita* extends from Massachusetts and northern Vermont westward across New York to southeastern Michigan, southwestward to eastern Kentucky, and southward along the Appalachian Mountains to northern Georgia, presenting a rather distinct and coherent pattern, except for the Georgia record (Map 1). Very likely the species ranges further northward, throughout New England and well into southern Ontario and Quebec and the Maritime Provinces. It will certainly be found more widely along the lower slopes of the Appalachian Mountains.

Seasonal Distribution.—Dates of collection of *scita* extend from the middle of September to the middle of February, but the one September record is from the northernmost locality from which the species is known (northern Vermont). The one October record and the single one from January are both from cave environments, while the February collection is from a southern but montane environment. All other records are in November and December, and even at the West Virginia locality most specimens were collected in December. From this evidence I am inclined to believe that there is only one generation per year.

Habitats.—This is the only species in which most of the specimens seen were taken from places other than the surface of snow. The most outstanding collection of *Chionea scita* is that made by Dr. M. S. Briscoe of Howard Univ., Washington, D.C. He set a number of traps in the floor of a cave near Harpers Ferry, West Virginia. These were baited with decomposing meat and were designed primarily to attract cavernicolous Coleoptera; however, he took 29 specimens of *Chionea scita* in addition to the other insects. This collection has been discussed earlier under the natural history of *Chionea*. Mr. Roger Sperka of the Univ. of Kentucky similarly found one female specimen in a cave in Kentucky. It would seem, therefore, that the occurrence of *scita* in fair numbers and well back from the cave entrance was no chance phenomenon and that having wandered into caves, these Chioneas might become at least semipermanent cave insects. Where I collected *scita* in southeastern Michigan, the habitat was a sparsely wooded shore of a marsh and the microhabitat a series of cavities in the loose soil and finely divided, decayed wood beneath a stump in the advanced stages of decay. The debris included, besides soil and wood particles, various other bits of plant matter, fragments of dead insects, etc., and although I found no sure evidence that the microhabitat was or had been a rodent nest, I would not rule out this possibility. The holotype of *C. primitiva* also was not found on snow but in leaf mold. The occurrence of *scita* at light in Pennsylvania is particularly interesting and has been discussed elsewhere under behavior of the adult flies.

Collection Records.—GEORGIA: Union Co., Vogel State Park, in pit-fall trap, elevation about 3200 ft, 10 Feb. 1972, J. Howell (1 ♀). KENTUCKY: Pulaski Co., Wind Cave (37°03′N, 84°31′W), elevation 840 ft, 24 Oct. 1970, R. Sperka (1 ♀). MASSACHUSETTS: Hampshire Co., Amherst, 13 Nov. 1933 (1 ♀); same, 14 Nov. 1933 (1 ♂); both collected by A. B. Gurney. MICHIGAN: Oakland Co., Highland Recreation Area, 4 mi E of Highland, 8 Nov. 1952, P. B. Kannowski (1 ♂); same locality, 12 Nov. 1952, G. W. Byers, D. Hynes, P. B. Kannowski (2 ♂, 2 ♀). NEW YORK: Cayuga Co., Owasco Lake, Cascade, in leaf mold, 15 Nov. 1915, Bishop and Crosby (1 ♂, holotype of

C. primitiva Alexander); Schuyler Co., Van Etten, Arnot Forest, Nov. 1927, R. D. Harwood (1 ♂); Steuben Co., Lake Keuka, Dec. 1905, Crosby collection (1 ♂); Sullivan Co., Surprise Cave, 11 Nov. 1966, S. Peck (1 ♀); Tompkins Co., Ithaca, 18 Nov. 1892, R. H. Petit (1 ♂); Ithaca, Needham's Glen, 12 Dec. 1932, J. G. Needham (1 ♂); Ithaca, 15 Dec. 1907 (1 ♂). ONTARIO: Waterloo, on melting snow, 19 Dec. 1977, L. Lesage (1 ♂). PENNSYLVANIA: Erie Co., Edinboro, tributary of Conneauttee Creek, 1465 ft, on outside of emergence trap, 8°C, 16 Nov. 1980, Becky Travis; Centre Co., State College (University Park), on window screen, 11 P.M., possibly attracted to light, 9 Nov. 1961, C. W. Rutschky (1 ♀). VERMONT: Chittenden Co., 6 mi N of Bolton (Upper Bryant Lodge), elevation 3000 ft, on snow, 14 Sept. 1954, Rodger Mitchell (1 ♀). VIRGINIA: Smythe Co., Lewis Fork at Rte. 603, 19 Jan. 1981, B. Kondratieff (1 ♂). WEST VIRGINIA: Jefferson Co., near Harpers Ferry, in cave, 8-15 Dec. 1939 (2 ♂); same, but 15 Dec. 1939 (13 ♂, 13 ♀); same, but 6 Jan. 1948 (1 ♂, 1 ♀); all collected by M. S. Briscoe.

Chionea wilsoni, NEW SPECIES

See Appendix 1.

THE **C. valga** GROUP

Body color in general reddish brown, grayish brown or dark brown; antennae with one to six flagellomeres beyond fusion segment; gonopophyses of male in form of upper horizontal blade (usually more or less impressed or bent downward in middle) with vertical keel and without slender apical hook; eighth abdominal tergum of female approximately half length of seventh tergum (or expanded at sides in *hybrida* and *stoneana*). Included species: *hybrida,* new species, *obtusa,* new species, *stoneana* Alexander and *valga* Harris.

Chionea hybrida, NEW SPECIES

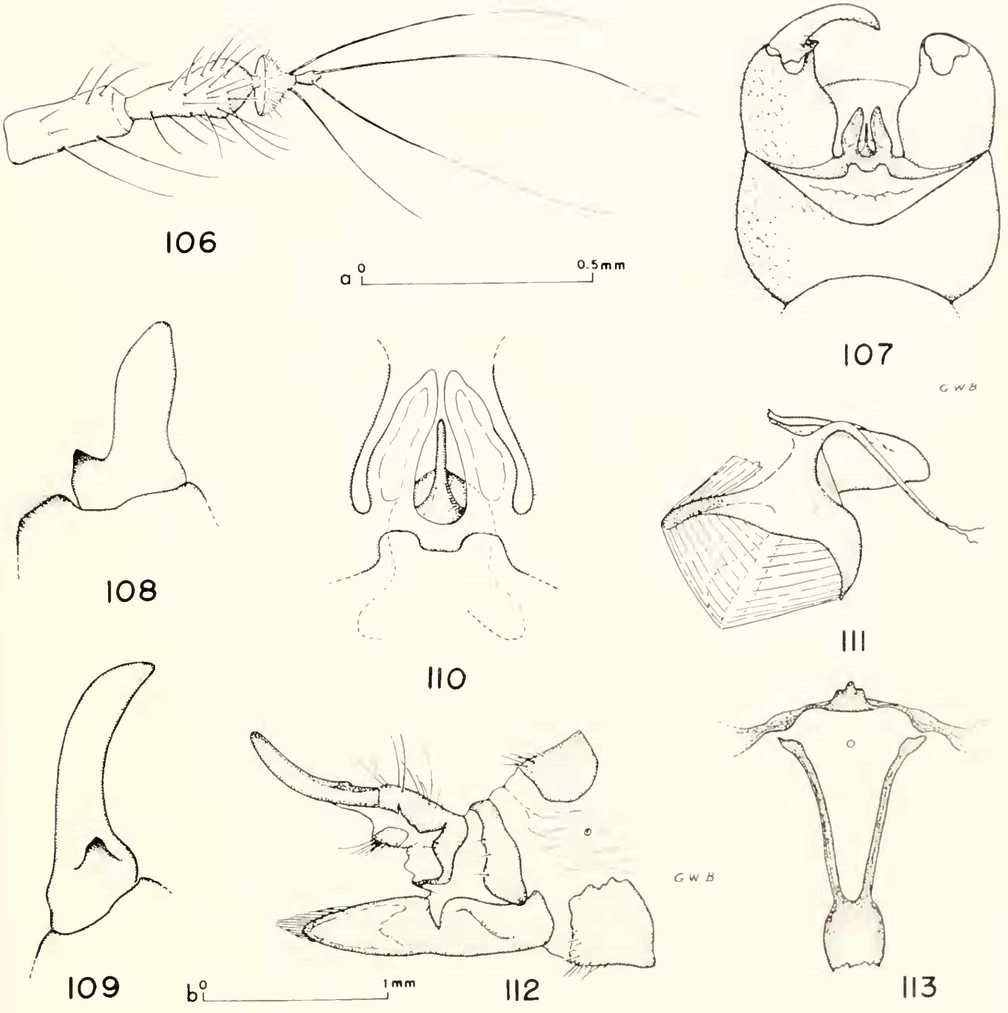
Diagnosis.—A western montane species of dark grayish brown color, with antennae having two or three flagellomeres; male gonapophyses elongate, concave dorsally, convergent apically, keeled ventrally; female cerci slightly longer than hypovalves, eighth tergum widened laterally.

Description (based on 2 ♂, 1 ♀, preserved in alcohol; 6 ♂, 11 ♀, pinned.—General appearance: Head including palps and antennae dark grayish brown, thorax dark brown to dark grayish brown, nearly black in dried specimens; abdominal sclerites brown to nearly black, ninth segment of male darker than other abdominal segments in specimens preserved in alcohol, all segments approximately same color in dried specimens; cerci of female dark amber colored; pleural membranes grayish in alcoholic specimens to dark grayish brown in pinned ones; fine, silvery pollinosity on head, thorax and to lesser extent on abdomen, visible in light from certain angles especially in dried specimens. Length of male about 2.9-4.9 mm; female about 4.4-5.9 mm, exclusive of antennae.

Head: Antennae (Fig. 106) consisting of subcylindrical scape, distally enlarged pedicel, short, broadly conical fusion segment, and usually one additional flagellomere bearing only two terminal setae. Eyes with about 110 facets in male, 100 in female.

Thorax: Halteres paler than dark grayish brown color of thoracic dorsum, pale grayish brown in alcoholic specimens, darker when dried. Legs brown to dark reddish brown, hairs long and thin (as is *C. valga*), not in distinct rows; in large males, hairs on femora, tibiae and basitarsi bent or slightly curled at apex, this less common in slender males and females; hairs of tibiae and basitarsi 1.3-1.5 times as long as diameter of segment. Tarsi generally same color as legs, but due to fine pubescence fifth tarsomere may appear darker than others in most lights.

Abdomen of male: Terga 1-8 sparsely hairy, corrresponding sterna slightly more hairy. Posterodorsal margin of ninth tergum (Fig. 107) broadly and smoothly emarginate, without lobes or prominences. Gonapophyses (Figs. 110, 111) elongate, convergent apically, each gradually tapering to narrowly rounded tip, with shallow, trough-like dorsal concavity and strong ventral keel; space between gonapophyses shaped like narrow-necked flask; penis arched upward at base, then curved downward, with two sinuate apical filaments. Basistyles thick, with inconspicuous, pilose posteromesal lobe. Dististyles (Figs. 108, 109) reddish brown, generally smooth-surfaced, glossy on outer curvature, much



FIGS. 106-113, *Chionea hybrida*. 106, right antenna, male holotype, dorsolateral aspect. 107, ninth abdominal segment, male holotype, dorsal aspect (left dististyle and hairs of left side omitted, tenth segment pushed inward). 108, right dististyle, holotype, ventrolateral aspect (apex concealed by curvature). 109, left dististyle, ventral aspect. 110, gonapophyses and penis, holotype, dorsal aspect (outline of apodemes of vesica indicated by dashed line). 111, right gonapophysis, penis, vesica and its apodemes and muscles, left lateral aspect (cut muscle connects to base of left gonapophysis). 112, terminal abdominal segments, female allotype, right lateral aspect. 113, ninth sternum and genital furca, allotype, ventral aspect. Scales: a—106, 108-111, 113; b—107, 112.

thickened at base with acutely pointed, darkly sclerotized mesal tooth, otherwise of generally uniform width throughout until near apex.

Abdomen of female: Segments 1-8 dark grayish brown, sparsely hairy. Eighth tergum widened (i.e., lengthened) at sides (Fig. 112). Upper and lower margins of hypovalves approximately equally curved toward apex. Cerci nearly straight in basal half, curved upward just beyond midlength, with tips rounded, not acute; cerci slightly longer than hypovalves (ratio 1.1:1). Arms of genital furca of approximately uniform thickness throughout, evenly divergent from basal portion; sides of basal portion curved outward slightly (Fig. 113). Median projection of ninth sternum with three teeth, middle one longest and most distinct.

Types.—Holotype, male, and female allotype, Temple Fork, Logan Canyon, Cache Co., Utah, 27 January 1968, W. D. Pearson and R. H. Kramer. Paratypes, 7 ♂, 11 ♀, as follows: UTAH: Cache Co., Logan Canyon, Temple Fork, 10 Feb. 1968, W. D. Pearson and R. H. Kramer (1 ♂, in alc.); Cache Co., Logan Canyon, Beaver Mountain, 20 Jan. 1974 (1 ♀); Cache Co., Logan Canyon, Sink Hollow, A.M., on ski tracks in fresh snow, 20°F, 7 Dec. 1974, T. and F. Whitworth (3 ♂, 6 ♀); Rich Co., in spruce-fir forest, 6 Dec. 1975 and 22 Jan. 1977, respectively, K. Smith (1 ♂, 1 ♀); Wasatch Co., 6 mi from U.S. Hwy. 40 near Strawberry River, 23 Nov. 1975, J. M. Payne (1 ♂, 3 ♀). IDAHO: Franklin Co., Franklin Basin, near Utah border, 14 Jan. 1978 (1 ♂). Holotype and allotype have been cleared but are not slide-mounted; paratypes pinned except as indicated. Holotype, allotype and 3 ♂, 3 ♀ paratypes in Snow Entomological Museum, Univ. of Kansas; remaining paratypes in collection of Utah State Univ., Logan, Utah.

Variation.—There is a third seta on the terminal flagellomere in a few individuals, but it is much shorter and more slender than the other two. About one-third of the specimens seen have two flagellomeres beyond the fusion segment. One male paratype has a small ventral tooth on the outer base of the dististyles. Variation in number, length and distribution of setae on head, thorax and abdominal sclerites is considerable, as typical for the genus. Similarly, both slender-legged males (e.g., one 2.9 mm long) and robust males (4.9 mm long) with much thickened femora exist, even in the small sample now at hand.

Relationships.—*Chionea hybrida* exhibits an unusual combination of taxonomic characteristics of the *valga* and *alexandriana* species groups; hence the name *hybrida.* The structure of the gonapophyses and absence of projecting lobes on the ninth tergum would place males of the species near *valga.* In the female the form of the eighth abdominal tergum resembles that of *valga,* and the abundant, long and slender setae of the legs give both males and females the general look of *valga* or *obtusa.* But the shape of the female's ninth sternum recalls that of *alexandriana* or *nigra.* Similarly, the very short antennal flagellum resembles that of some species in the *alexandriana* group that occur in the western states, yet in *stoneana* one finds the flagellum equally reduced. Males of *C. hybrida* may readily be differentiated from those of other western species by reference to the ninth tergum, gonapophyses and antennae; females, which somewhat resemble *nivicola* in form of eighth tergum, or *jellisoni* in having short antennae and rather short cerci, may be separated from these species by the fuzzy appearance of the setae on the legs and usually, as well, by the antennal structure.

Geographic Distribution.—At present, *C. hybrida* is known only from the northern Wasatch Range of northern Utah and adjacent Idaho (Map 3). Its actual range probably does not extend very far beyond this, perhaps a little farther south and north along these mountains and possibly eastward into the Uinta Mountains. The range as now known falls within that of *C. jellisoni* and adjoins the westermost extension of the range of *C. nigra*.

Seasonal Distribution.—There is probably a single annual period of adult emergence prolonged over about three months. The few specimens known were taken in only eight collections fairly evenly spread over the period from late November to early February.

Habitats.—In general, the region in which *C. hybrida* lives is one of western yellow pine (ponderosa pine) and Douglas fir. The habitat in Rich Co., Utah, is described as spruce-fir forest. Elevations at some of the collection sites are: along Temple Fork, about 1830 m or 6000 ft; in Sink Hollow, upper Logan Canyon, 2225 m (7300 ft); approximately 2256 m (7400 ft) along the Strawberry River; and probably above 2450 m on Beaver Mountain (summit 2698 m). Most if not all of the specimens were taken from the surface of snow.

Chionea obtusa, NEW SPECIES

Diagnosis.—A western species, brown to grayish brown in color, with antennae having five to seven flagellomeres; male gonapophyses, seen from above, broad, deeply concave, with rounded tips, ventral keel with a ventral subapical process; female cerci short, broad, with bluntly rounded, upturned tips; setae of legs long, slender, abundant.

Description (based on 2 ♂ and 3 ♀ on slides, 3 ♀ pinned, and 25 ♂ and 21 ♀ in alcohol).—General appearance: Head dark brown, thorax brown to grayish brown; abdominal sclerites light brown to light grayish brown, except ninth segment of male dark brown, cerci of female yellowish; pleural membranes tan. Length of male about 4-7 mm, female about 4.5-8 mm, exclusive of antennae.

Head: Antennae (Figs. 114, 115) consisting of scape, pedicel and five to eight flagellomeres (six in holotype); fusion segment asymmetrically short-conical,. about as long as greatest diameter or a little shorter. Hairs of vertex and clypeus soft, slender, not blackened. Eyes with about 80 ommatidia each.

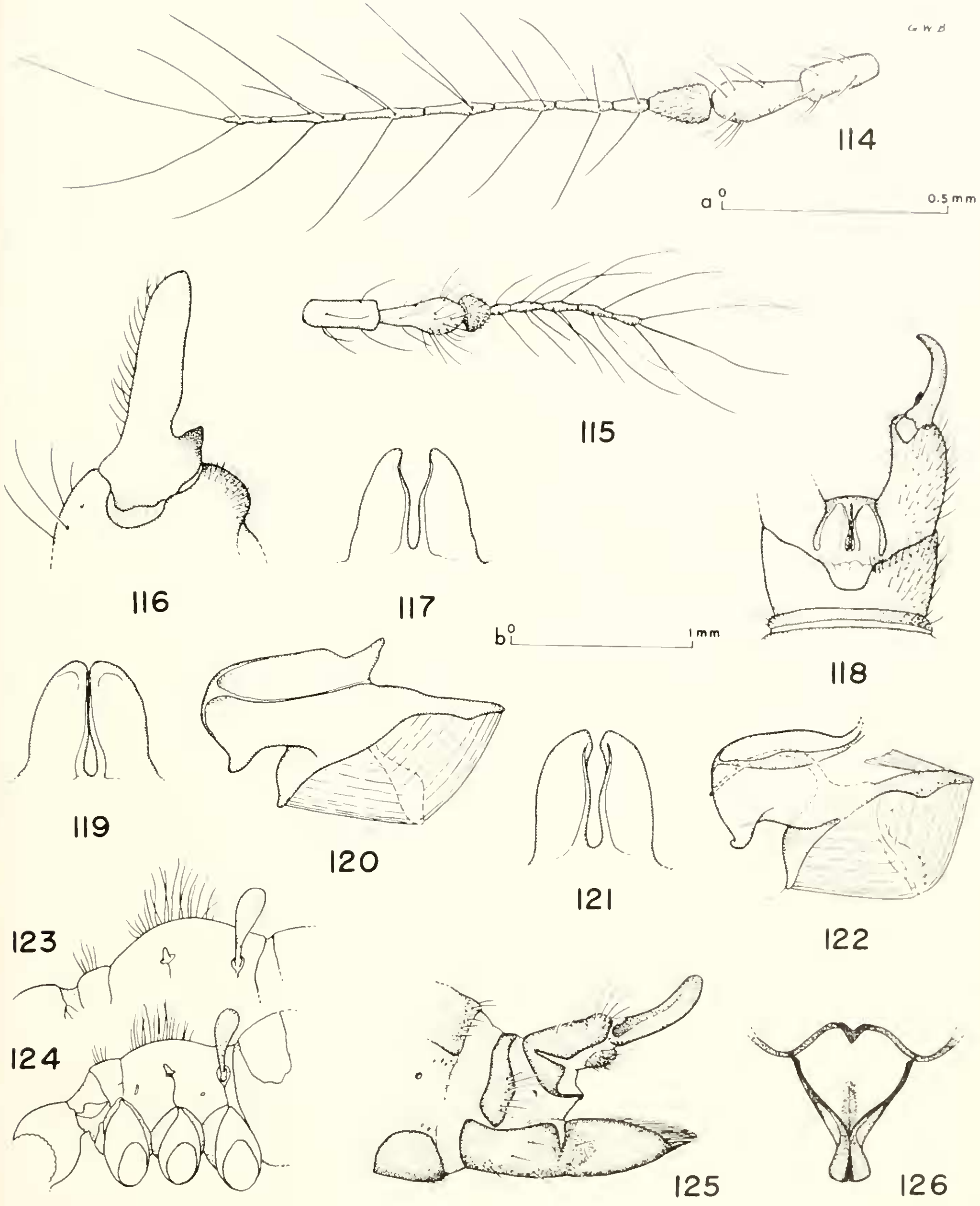
Thorax: Halteres light brown to gray. Legs brown to grayish brown, with approximately six dorsal and five ventral rows of long femoral setae in males, four dorsal and three ventral in females; in males, additional small setae often present, not in clearly defined rows; tarsomeres beyond basitarsi slightly darker than legs. Notal and coxal setae slender, not blackened.

Abdomen of male: Terga 1-6 with long, thin hairs on posterior half, terga 7-8 with hairs in single submarginal row; terga without distinct color pattern. Hairs of sterna chiefly along posterior margins, most dense on posterolateral corners. Ninth tergum (Fig. 118) with broadly U-shaped emargination, a low, wide, scarcely evident lobe at each side of emargination; six to nine setae in approximately transverse row on each lobe, in alignment with more lateral setae of tergum. Gonapophyses (Figs. 117, 119, 121), seen from above, broad, blade-like with upturned lateral margins, thus deeply concave on dorsal surface, with broadly to narrowly rounded tips; deep ventral keel of each gonapophysis with incurved, subapical projection; mesal margins slightly divergent basally, subparallel to slightly divergent in apical half; apex of penis slightly flared, without terminal filaments. Basistyles slender to moderately thick for genus, each with bluntly rounded, pilose posteromesal lobe. Dististyles (Fig. 116) light brown, slender, rather evenly curved, only slightly thickened at base, with single prominent, blackened mesal tooth separated from base by distinct notch. Base of tenth segment about as wide as emargination of ninth tergum, segment not abruptly narrowed near mid-length, only lightly sclerotized laterally.

Abdomen of female: Tergal and sternal hairs shorter, more widely scattered over sclerites than in male. Eighth tergum about one-third to one-half as long as seventh, widest at sides, with three or four setae along posterolateral margins (Fig. 125). Hypovalves of eighth sternum short, deep, with ventral margin curving upward, dorsal margin only slightly curved downward to subacute apex. Arms of genital furca broad at base, tapering toward mid-length, slender in apical half, widely divergent (Fig. 126); basal portion not strongly sclerotized except medially, constricted near its mid-length; wide, elongate section of lining of bursa copulatrix visible in cleared specimens (shown as stippled zone in Fig. 126). Ninth sternum formed by junction of slender, darkly sclerotized bands at acute, downward-curved point. Tenth tergum with long setae on posterior margin, otherwise mostly bare. Cerci (Fig. 125) short, thick, only about 3-4 times as long as greatest width, widest near base but when seen from side appearing slightly widened beyond mid-length, upturned in apical half to bluntly rounded tips, subequal in length to hypovalves, measured from notch to tip.

Types.—Holotype, male, Cranbrook, British Columbia, elevation about 1000 m, 17 Nov. (year not recorded), C. B. D. Garrett; on microscope slide no. 6152. Allotype, female, same data as holotype; on slide no. 6162. Paratypes, 27 ♂, 26 ♀, as follows: BRITISH COLUMBIA: Cranbrook, 1 Nov. (1 ♂, 1 ♀, on slides), 2 Nov. (1 ♀), 14 Nov. (1 ♀), 3 Dec. (1 ♀), C. B. D. Garrett. ALBERTA: Boulder Pass, 7490 ft, Banff Nat. Park, on 12-in-deep snow, 14 Oct. 1968, K. W. Richards (2 ♀); Lake Louise, Banff Nat. Park, 6500-7000 ft, 4 Oct. 1973, J. A. Downes (4 ♂, 3 ♀). IDAHO: Benewah Co., Heyburn State Park, 20 Dec. 1975, Albert Greene (1 ♂); Idaho Co., Clearwater Nat. Forest, Mud Creek Jct., 25 Nov. 1978, R. C. Biggam and M. A. Maurer (6 ♂, 4 ♀). MONTANA: Gallatin Co., Taylor Fork, 7500 ft, 1 Nov. 1932, R. E. Wall (1 ♀); Missoula Co., Holland Lookout, Seely Lake, 8012 ft, 4 Oct. 1952, J. A. Chapman (1 ♀); Missoula, on snow, temp. about 32°F, 21 Dec. 1952, J. A. Chapman (1 ♀); Missoula Co., Elk Creek, Lubrecht Forest, 4000 ft, 22 Jan. 1972, R. A. Haick (16 ♂, 12 ♀); Ravalli Co., near Sleeping Child Hot Spring, on 1 ft of snow, 16 Jan. 1972, W. L. Jellison (2 ♂, 1 ♀). OREGON: Wallowa Co., Wallowa-Whitman Nat. Forest, Eagle Cap Wilderness, 6000-7000 ft, weather clear, 24 Nov. 1972, Albert Greene (1 ♂). Holotype, allotype and topotypic paratypes are in the Museum of Zoology, Univ. of Michigan, Ann Arbor, Michigan. Paratypes are in the U.S. National Museum of Natural History (including the C. P. Alexander collection), the Snow Entomological Museum, Univ. of Kansas, and the collections of Washington State Univ., Univ. of Idaho, and Univ. of Alberta. I have also seen 1 ♂ from Sheep Creek, Windermere, British Columbia, 10 Oct. 1927, A. A. Dennys, in the collection of Agriculture Canada, Ottawa; and 1 ♂, 20 Nov 1932, from Edmonton, Alberta, collected by E. H. Strickland, in Dr. Alexander's collection. These two specimens, the first pinned, the second on a slide, have not been made paratypes because I was not able to check certain of their structural details; however, I am reasonably confident of their identification. One further male, from Glacier National Park, British Columbia, Nov. 1975, collected by J. G. Woods, could be positively identified but is considered too damaged to be made a paratype.

Variation.—Among the paratypes from Elk Creek, Montana, males range from 4.0-6.8 mm (mean = 5.3) (one individual 3.5 mm long has a distorted, extremely telescoped abdomen and appears in other ways about the same size as the 4.0 mm



Figs. 114-126, *Chionea obtusa.* 114, left antenna, large male from Idaho, lateral aspect, showing seven flagellomeres beyond fusion segment. 115, right antenna, male holotype, lateral aspect. 116, left dististyle and apex of basistyle, male from Idaho, posterior (ventral) aspect. 117, gonapophyses, male from British Columbia, dorsal aspect. 118, ninth abdominal segment, male from British Columbia, dorsal aspect (most of right side omitted). 119, gonapophyses, male from Idaho Co., Idaho, dorsal aspect. 120, same, right lateral aspect. 121, gonapophyses, male from Boise Co., Idaho, dorsal aspect. 122, same, right lateral aspect. 123, thoracic dorsum, male, left lateral aspect. 124, thorax, female, left lateral aspect; compare with *C. valga,* Figs. 139, 140. 125, terminal abdominal segments, female, left lateral aspect. 126, ninth sternum and genital furca, female, ventral aspect. Scales: a—114-117, 119-122, 126; b—118, 123-125.

male); females range from 4.5-7.7 mm (mean = 5.8). Small males have slender femora, are relatively sparsely hairy on legs and body, and have slender basistyles. Large males are robust, with incrassate femora, very hairy legs and body, and have thickened basistyles, which, however, are plainly longer than wide, not short and thick as sometimes seen in robust males of *C. alexandriana* and some other species. Males of intermediate length are also intermediate in hairiness, enlargement of femora, and robustness of the ninth abdominal segment. Comparison of measurements of various structures in the smallest and largest males yields some interesting ratios: body length, .59 to 1; length of hind femur, .30 to 1; length of genital bulb, .83 to 1.

All females, whether relatively large or small, are slender-legged. Both large females and small ones have about the same size of eggs (which are usually discernible through the abdominal pleural membrane in alcoholic specimens). Ratios of smallest to largest measurements are as follows: body length, .58 to 1; length of hind femur, .59 to 1; length of cercus, .83 to 1; length of hypovalve, measured from notch to tip, .91 to 1.

These ratios for both males and females demonstrate that despite rather conspicuous variation in some aspects of size, all adults retain reproductive structures of roughly uniform size. Dimensions of the ovipositor are probably influenced by those of the eggs. And for a male to be functional in copulation, his genital structures must accommodate to those of the female, no matter how much other measurements may vary. It is not clear why the observed variation in size exists, but there is probably rather strong selection for reproductive apparatus of "normal" proportions.

Variation in shape of the male gonapophyses and of the space between them, as seen from above, may result in part from slight outward twisting of their tips or compression between the basistyles (Figs. 117, 119, 121).

About 65% of the specimens from British Columbia have four flagellomeres beyond the fusion segment, the others five. In the large sample from Elk Creek, Montana, roughly 40% (among both sexes) have four flagellomeres beyond the fusion segment, while 60% have five. Farther to the south and west, six flagellomeres in addition to the fusion segment is the common condition, with seven found in three robust males. There is thus a clinal increase in number of flagellomeres from north to south.

The holotype is a robust male having incrassate femora, especially on the hind legs, and a wider ninth segment and thicker basistyles than most other males. It also has many femoral setae outside the discernible rows. Femoral and tibial setae, especially in robust males, may be curly at the tips as in *C. valga*. Other variation noted has been included in the description.

Relationships.—The close affinity of *Chionea obtusa* with *C. valga* Harris is shown by the similarity of structure of the gonapophyses and dististyles in the male, the eighth tergum and genital furca in the female, and of the antennae and the hairs of head and body in both sexes. Males of the two species can be distinguished by the ninth abdominal tergum, which is distinctly emarginate medially in *obtusa* but so broadly emarginate as to be virtually entire in *valga*. Both males and females of *obtusa* have the mesonotum only slightly downcurved to the pronotum (Figs. 123, 124), while in *valga* the mesonotum is conspicuously humped, that is, abruptly downcurved to the pronotum (Figs. 139, 140). Females of *obtusa* are readily recognized by their short, bluntly tipped cerci, which are unlike those in any other species, and to which the specific name refers. *Chionea obtusa* also bears some resemblance to *C. nivicola* Doane, with which it sometimes occurs. This is based largely on the similar number of antennomeres. In males of *nivicola* the gonapophyses are essentially compressed, that is, flattened, vertically oriented blades, and the ninth tergum bears prominent lobes. *Chionea obtusa* also has longer, finer and much more abundant hairs and setae on body and legs than are found in *C. nivicola.*

Geographic Distribution.—The known range of *C. obtusa* extends from the plains of central Alberta to the Rocky Mountains of southeastern British Columbia and adjacent Alberta, to western Montana, northern Idaho and northeastern Oregon, some eight degrees of latitude and four of longitude (Map 3). Although apparently restricted to mountainous areas (up to 2300 m) in most of its range, *obtusa* occurs near 675 m in the vicinity of Edmonton.

Seasonal Distribution.—Dates of collection are in every month from October through January, but separate collections are scarcely numerous enough to show any clear pattern of emergence of adults. Some other western species that are found in autumn (October-November) have a second period of emergence in spring (March-April), and further collecting may well show that this is true also of *Chionea obtusa.* The fact that the entire range of *obtusa* is northern, for the genus, may influence seasonal appearance of adults.

Habitats.—For most of the specimens, no ecological field data are available. The range is generally within the zone of Douglas fir, western yellow pine (ponderosa pine), lodgepole pine, larch and western white pine. The records for Edmonton, however, are possibly from tall grass prairie, which occurs in the immediate vicinity of that city. There is, of course, some possibility that Strickland labelled as "Edmonton" some specimens taken in the nearby subarctic forest of spruce and fir. Most specimens were taken on snow, it appears, and most in wooded areas. The elevational variation in habitats has been mentioned above.

Chionea stoneana Alexander

Chionea stoneana Alexander, 1940: 100-102; Alexander, 1965: 72.

as *Chionea valga*: Lugger, 1896: 230-231 (misidentification).

Diagnosis.—A mid-western species with antennae having three (rarely only two) flagellomeres; male gonapophyses elongate, subparallel blades with acute tips; female cerci strongly upturned in apical half, setae of legs short, not in clearly defined rows.

Description.—General appearance: Head dark brown to blackish brown, thorax blackish brown, slightly paler medially; abdominal sclerites grayish brown, terga slightly darkened laterally; ninth segment of male and eighth through tenth segments of female, except hypovalves, dark brown, cerci grayish amber; pleural membranes pale grayish brown. Length of male about 2.3-5.7 mm, female about 2.3-5.9 mm, exclusive of antennae.

Head: Antennae (Figs. 127, 128) consisting of scape, pedicel and three or rarely two flagellomeres; fusion segment subconical, asymmetrical, usually a little longer than greatest diameter. Setae on vertex pale. Eyes with about 100-120 ommatidia each.

Thorax: Halteres pale grayish brown (in alcohol), contrasting conspicuously with color of thoracic dorsum. Legs grayish brown; femoral and tibial setae more numerous than in most other species, short, pale brown, each arising from a low papilla, not serially arranged, or at least not in clearly defined rows; setae at apical ends of femora and tibiae longer than others; basitarsi of male darkened apically, succeeding segments grading from dark brown to blackish brown on terminal segment; tarsi of female only slightly darker than legs. Setae of pronotum and mesonotum elongate, not blackened.

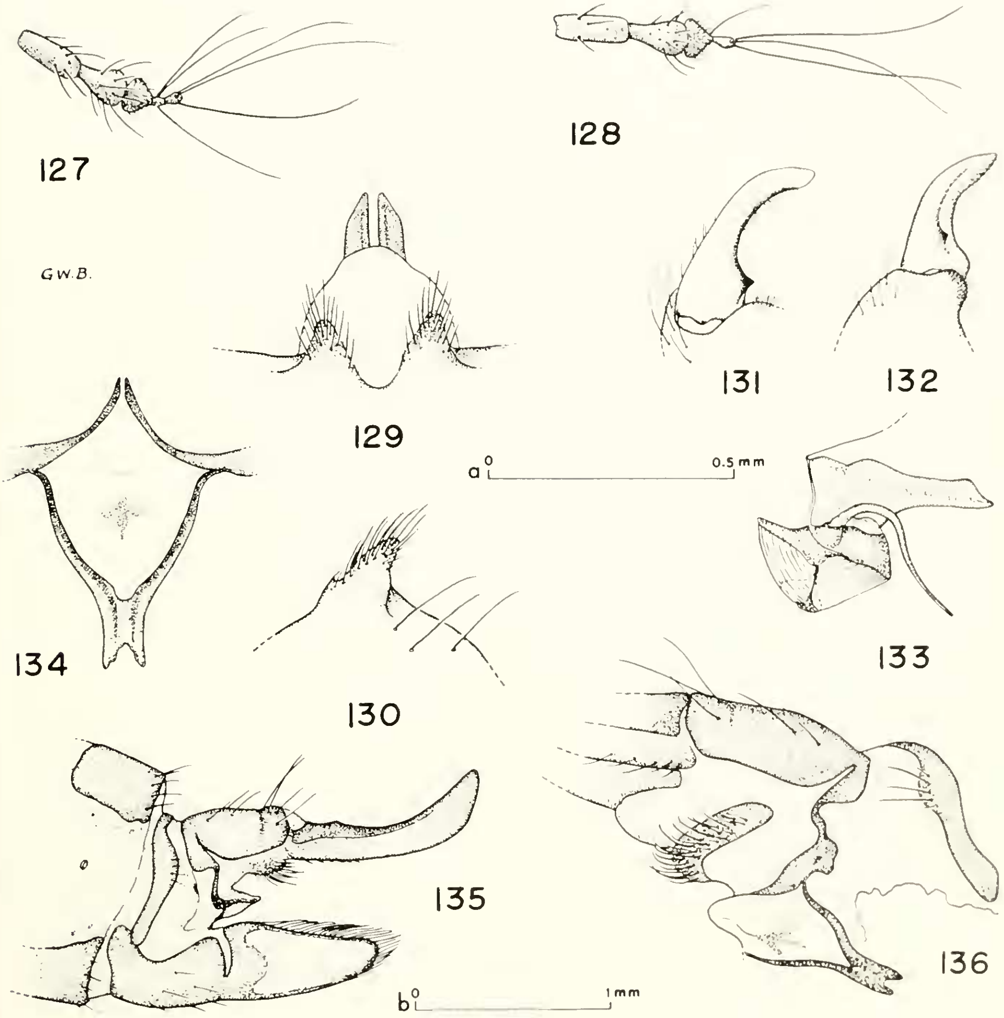
Abdomen of male: Posterodorsal margin of ninth tergum (Fig. 129) bearing two prominent, blackened, setiferous lobes, with V-shaped to U-shaped space between them; lobes projecting noticeably dorsad (Fig. 130), each bearing about 12 (8-14) brownish setae. Gonapophyses, seen from above (Fig. 129), elongate, parallel-sided, protruding from genital chamber, concave on dorsal surface, keeled ventrally, with sharply pointed apices; space between gonapophyses very narrow, slightly widened at base; penis not curved upward from floor of genital chamber (Fig. 133), unmodified at apex. Basistyles moderately thick in smaller males to thick in robust males; posteromesal lobe of each prominent, evenly rounded, hairy. Dististyles (Figs. 131, 132) dark yellowish brown to dark brown, broad at base, with prominent, darkened, subacute mesal tooth, then abruptly narrowed, somewhat unevenly curved to narrowly rounded tip; darkly sclerotized ridge extending distad from mesal tooth; ventral tooth not present in specimens examined. Tenth segment rather evenly tapered from base toward apex, lightly sclerotized and pigmented laterally and ventrally.

Abdomen of female: Eighth tergum short (i.e., slender) dorsally, irregularly widened laterally but only to approximately one-third length of seventh, with three to five posterolateral setae. Hypovalves of eighth sternum subhyaline except for dark amber-colored margins, moderately deep for genus, with dorsal margin more or less straight or slightly concave, ventral margin tapering evenly toward dorsal for most of its length, then near apex sharply upturned to rounded tip (Fig. 135). Arms of genital furca slightly wider basally than apically, often pale (less darkly sclerotized) along one side or the other (Fig. 134); basal portion of furca longer than wide, not strongly sclerotized medially; entire structure lyriform. Ninth sternum formed by convergence of two slender, darkly sclerotized bands (Fig. 134) on upper surface of rounded projection, widened near attachment to furca (Fig. 136); acute point of convergence sometimes less densely sclerotized than rest of bands. Bursa copulatrix of large diameter, lightly sclerotized for much of its length (Fig. 42), with blackened swellings at bases of dorsal spermathecal ducts (visible through membrane between arms of furca). Cerci of medium length for genus, about 5-5.5 times as long as greatest width, thick, strongly curved upward in apical half, slightly widened just beyond mid-length, then narrowed to acutely rounded apex (Fig. 135); cerci about 1.2-1.4 times as long as hypovalve measured from notch to tip.

Types.—Holotype, female, Urbana (Champaign Co.), Illinois, in mouse nest, 11 December 1938, Philip C. Stone collector. Allotype, male, same locality as holotype, from nest of field mouse, *Microtus ochrogaster,* 16 December 1939, P. C. Stone. Paratopotypes: 1 ♀, from mouse nest, 12 January 1939; 1 ♂, 1 ♀, from mouse nest, 2 February 1940. The holotype, allotype and male paratype are mounted on microscope slides in the collection of Dr. C. P. Alexander, Amherst, Massachusetts. One female paratype in alcohol is in the collection of the Illinois State Natural History Survey, Urbana; the other is in the Museum of Comparative Zoology, Harvard Univ. I have examined all the types.

Variation.—Several individuals among the many examined had a single flagellomere beyond the fusion segment (Fig. 128); these were the one from Oklahoma, one male each from Iowa and Wisconsin, and two males, three females from near the type locality in Illinois. Some aspects of color variation have been included in the description, but a few others deserve mention here. When alive, *Chionea stoneana* has a decidedly sooty gray color, which may persist in specimens preserved dry. This leads me to wonder if the flies from Minnesota described by Ainslie (1906) as *C. valga* might not have been *stoneana.*

Since I have not been able to locate those specimens, and since the locality is reasonably within the range of both *valga* and *stoneana*, I have accepted his identification. Length of most males is in the range 4-5.5 mm, but one pinned specimen from Columbia, Missouri, is only 2.3 mm long, although somewhat shriveled, the abdominal segments "telescoped." In most males preserved in alcohol, the median region of the ninth abdominal tergum is a little paler than the rest of that segment, but in a few it was conspicuously paler, being almost yellowish brown and having the appearance of a median stripe. Teneral individuals preserved in alcohol are pale



FIGS. 127-136, *Chionea stoneana*. 127, left antenna of male allotype, lateral aspect. 128, antenna of male from Oklahoma, showing single flagellomere beyond fusion segment. 129, posteromedian portion of ninth abdominal tergum, membranous tenth segment, and apices of gonapophyses, male, dorsal aspect. 130, posteromedian lobes of ninth tergum, left lateral aspect. 131, left dististyle, ventral aspect. 132, left dististyle, ventromesal aspect (more robust male than shown in Fig. 131). 133, right gonapophysis, penis, vesica and its apodemes and muscles, left lateral aspect (left gonapophysis removed). 134, genital furca and ninth sternum, female, ventral aspect (cleared, slide-mounted specimen). 135, terminal abdominal segments, female paratype, left lateral aspect. 136, details of ninth and tenth abdominal segments, female, ventrolateral aspect. Scales: a—127-134, 136; b—135.

tan, the integument so weakly pigmented that the muscles can be seen through it. The gonapophyses may taper evenly toward the apices, but in many males they have a more uniform width for most of their length, then narrow rather abruptly to acute tips. In the female, the expanse of the genital furca varies somewhat, and the intensity of sclerotization in its basal portion is highly variable, producing margins or other zones of lighter brown contrasting with the dark bases of the arms.

Relationships.—In defining the *valga* species group, near the outset of this report, I was obliged to stretch its limits somewhat to include *Chionea stoneana.* This was due primarily to the great reduction in the number of antennal segments in *stoneana* and *hybrida,* the other species in the group having five or more flagellomeres. The shape of the eighth abdominal tergum in the female of *stoneana* likewise is not in close conformity with that of the other species in this group. On the basis of the structure of the male gonapophyses, however, *stoneana* appears to belong in the *valga group,* this placement being supported by such details as the number of spermathecae and enlarged, sclerotized bursa copulatrix in the female and shape of the tenth segment in the male. The ninth abdominal tergum of the male most nearly resembles that of *C. nivicola* Doane, and neither of the two species has the ventral tooth on the dististyles; but the gonapophyses of *stoneana* are more like those of *valga* or *obtusa.* The pale, short, thick setae of body and especially legs suggest a relationship with *nivicola,* but the number and distribution of these on the femora and tibiae will serve to differentiate *stoneana* from all other species. I think that the resemblance to *Chionea alexandriana* and species in the *alexandriana* group on the basis of the antennae (cf. Alexander, 1940: 101) is only superficial and that the other characters of *stoneana* mentioned above more accurately indicate its relationships.

Geographic Distribution.—In the 40 years since the description of this species, it has never again been recorded, although it occurs in a region of considerable entomological activity. After discovering that at least some of Lugger's specimens from Minnesota were *stoneana* and not *valga* and then finding, among borrowed specimens, one from Norman, Oklahoma, I became convinced that the species must be widespread on the eastern plains, although possibly confined to wooded areas. I searched for it in Kansas in the winters of 1956 through 1960 and urged my students to watch for it. In the winter of 1960-1961, Mr. George Singer, to whom I had shown specimens of *Chionea* only a few days earlier, brought in three males of *stoneana* from Franklin Co., Kansas. The localities from which *stoneana* is now known are widely scattered and give only a suggestion of the range of the species, but I would expect to find it in the plains from Canada to northeastern Texas and eastward to Ohio, central Kentucky and possibly even in the Ozark Mountains of Arkansas (Map 3).

Seasonal Distribution.—The few available collection dates span the period from early November to early February, with records in all four months. Most specimens taken in early November are teneral. I am inclined to believe that there is but one generation a year and that the long season in this case reflects the longevity of the adults. The appearance of *Chionea stoneana* as far south as central Oklahoma at the earliest collection date is difficult to explain on the basis of my present concepts, unless 1926—the year of that collection—was unusually cold. However, as more data are gathered about the geographic and seasonal distribution of *stoneana,* this early, southern record may prove to be not at all unusual.

Habitats.—In Kansas, I found *Chionea* *stoneana* in two apparently abandoned mouse nests situated in excavations beneath large, sawed sections of logs that had been lying on the ground for many months. The area had been partially deforested and was being used as a pasture. The woods were predominantly oaks, with some hickory and locust, and enough trees remained to have cast overlapping shadows on most of the ground during summer. The ground cover was grasses, various weeds of low to medium height, and some brush. Several logs were rolled over in the search for mouse nests or other cavities, but only the larger ones (about 20 in in diameter and, in these instances, 2-3 ft long) had been utilized as shelters by the rodents. Searching carefully under smaller logs, among dead leaves, in brush piles, etc., yielded no Chioneas, and none was seen on the ground, even near the nest logs. The mouse nests contained finely shredded, decayed wood, not unlike sawdust but the shreds a little coarser and more elongate, mixed with scraps of dead leaves, grass stems, and loose soil. The adult insects were mostly near the surface of this material, but digging down a few inches exposed additional individuals, as well as larvae in various instars. The temperature one inch below the surface of the nest material was 36°F, the air temperature 34°F. Other arthropods found beneath these nest logs included wood roaches, ants, *Myodocha* lygaeids, and a machilid, all scarcely able to move when exposed, and some small staphylinid beetles that were as active as the Chioneas.

As mentioned above, the type series of *stoneana* were all collected from mouse nests, including nests of the prairie field mouse, *Microtus ochrogaster* Wagner. The Minnesota specimens were found on the surface of snow, ". . . as far as observed only after a fresh fall of snow" (Lugger, 1896). Dr. Lugger also recorded that the flies were usually seen when the temperature was near freezing but that ". . . some have been found when it was below zero and the surface of the snow was frozen into a solid crust." There are several recent collections made by pitfall traps and Malaise traps, both effective in the absence of snow cover.

Collection Records.—ILLINOIS: Champaign Co., Urbana, in nests of mouse, *Microtus ochrogaster*, 11 Dec. 1938 (1 ♀, holotype), 16 Dec. 1939 (1 ♂, allotype), 2 Feb. 1940 (1 ♂, 1 ♀), all collected by P. C. Stone; Champaign Co., 2 mi N of Homer and 1.5 mi W of Route 49 bridge on Salt Fork of Vermilion River, 7 Nov.-2 Dec. 1972, in pitfall trap in oak-hickory woods, J. D. Unziker (8 ♂, 9 ♀); Clark Co., Rocky Branch, NE of Clarksville, 5 Feb. 1965, Rotrammel and Braasch (1 ♂); DeWitt Co., Allerton Park, 27 Dec. 1969, J. Bouseman and R. Selander (3 ♂); Jackson Co., Carbondale, on lighted window, 11 p.m., temperature 30-32°F, 24 Dec. 1960, J. C. Downey (1 ♂); Randolph Co., Fort Kaskaskia State Park, on snow, 15 Jan. 1964, L. J. Stannard (1 ♂). INDIANA: Clay Co., Posey Twp., in pitfall trap, old field, 23-26 Dec. 1974, J. R. Munsee (1 ♂, 1 ♀). IOWA: Boone Co., Ledges State Park, in oak-hickory leaf litter on ground near Pease Creek, 7 Nov. 1967, H. D. Blankespoor, L. C. Lewis and R. L. Jacques (3 ♂, 1 ♀, all teneral); Ledges State Park, 19 Jan. 1968, D. J. Kotzin (1 ♂, 1 ♀). KANSAS: Douglas Co., Breidenthal Reserve, Univ. of Kansas, 2 mi N of Baldwin, alive in pitfall trap, 20 Jan. 1973, G. W. Byers (1 ♂); Franklin Co., 14.5 mi S of Lawrence, from old mouse nests, 18 Dec. 1960, G. Singer (3 ♂); 2 Jan. 1961, G. W. Byers (14 ♂, 5 ♀). MINNESOTA: Ramsey Co., St. Paul (St. Anthony Park), December ("about Christmas"), O. Lugger (1 ♂, 1 ♀, and probably other specimens not seen). MISSOURI: Boone Co., Columbia, USDA Laboratory grounds, in Malaise trap, Feb. 1971, F. D. Parker (1 ♂, unusually small); Columbia, in Malaise trap, 4 p.m.-7 a.m., 21-22 Dec. 1961, F. D. Parker (1 ♂, 1 ♀); St. Francois Co., Womack, 16 Jan. 1964, on snow, L. J. Stannard (1 ♀). OKLAHOMA: Cleveland Co., Norman, 11 Nov. 1926, M. J. Brown (1 ♂). WISCONSIN: Iowa Co., Clyde Twp., Sec. 12, from nest box CH3-1, 23 Dec. 1968, J. O. Jackson (1 ♂).

Chionea valga Harris

Chionea valga Harris, 1835: 595 (nomen nudum).

Chionea valga Harris, 1841: 404-405; Harris, 1852: 482; Harris, 1862: 601, Fig. 260; Osten Sacken, 1869: 168-170; Osten Sacken, 1878: 29; Lugger, 1896: 230-231 (in part *C. stoneana*); Ainslie, 1906: 275-276; Johnson, 1907: 41-43, with figs.; Washburn, 1907: 103; Needham, 1908: 207; Johnson, 1912: 102-104; Alexander, 1917: 207; Alexander, 1919: 805, 903; Treherne, 1920 (misidentified—*C. alexandriana*); Crampton, 1925: 204 ff., Fig. 9; Leonard, 1928: 694; Alexander, 1942: 429; Alexander, 1956: 177; Byers, 1961*a*: 190, Fig. 1; Byers, 1963: 160; Alexander, 1965: 72.

Chionea aspera Walker, 1848: 82; Alexander, 1919: 903.

Chionea gracilis Alexander, 1917: 206, Fig. 2; Alexander, 1919: 903; Leonard, 1928: 694; Alexander, 1942: 428-429.

Chionea noveboracensis Alexander, 1917: 205-206; Alexander, 1919: 903; Leonard, 1928: 694; Alexander, 1942: 429 (new synonymy).

Chionea waughi Curran, 1925: 24-26; Alexander, 1942: 429.

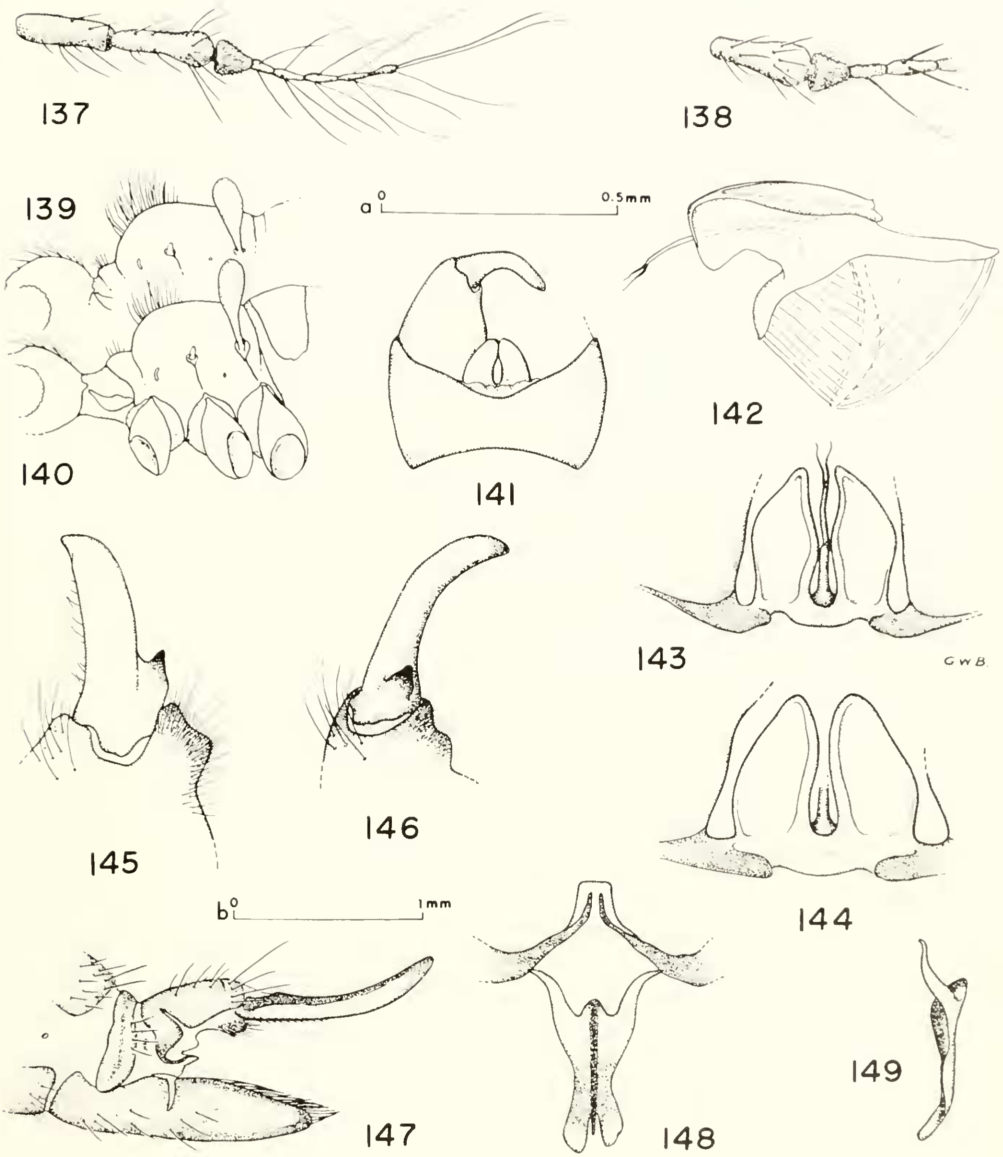
Diagnosis.—A northern and eastern species of dull reddish brown to grayish brown color, with antennae of seven or eight segments; male gonapophyses, seen from above, broad, shallowly concave, blade-like, with concealed, deep ventral keel; female cerci slightly widened and upturned beyond mid-length, then tapered to acute apex; median portion of ninth sternum weakly sclerotized, truncate apically.

Description.—General appearance of specimens preserved in alcohol: head dark reddish brown, thorax and abdominal sclerites reddish brown to brown, except ninth segment of male dark reddish brown; membranous areas paler brown; cerci of female dark amber-brown. Specimens preserved dry (on pins) more grayish brown in color. Length of male about 3.5-6.0 mm, female about 4-8 mm, excluding antennae.

Head: Antennae (Fig. 137) with pedicel slightly longer than cylindrical scape; fusion segment subconical, asymmetrical, about as long as its basal diameter; four or five additional flagellomeres. Setae on vertex dark brown, stout. Eyes each with about 100-130 ommatidia.

Thorax: Dorsum mostly reddish brown to brown, darkening unevenly to sides, on pronotum and on metanotum. Mesonotum in both sexes conspicuously "humped" in lateral aspect, with anterior slope nearly perpendicular to pronotum (Figs. 139, 140). Setae on mesonotum numerous, long, erect. Halteres grayish brown, contrasting with color of thoracic dorsum but not conspicuously so. Legs of moderate length, with hind femora extending only approximately to end of abdomen; femora light reddish brown to dark yellowish brown, their setae long, attenuate at tip, brown, not in readily discernible rows in males, usually in four dorsal, three ventral rows in females. Tibiae and basitarsi same color as femora, with almost equally long, slender setae; tibial setae of females and of fore and middle legs of males generally in longitudinal rows, more randomly distributed on hind legs of males. Tarsomeres beyond basitarsus darkening to brown.

Abdomen of male: Tergal setae long, pale, sparse, chiefly near posterior margins of terga. Sternal setae longest and most dense at sides of sterna, with a few along posterior margins. Posterodorsal margin of ninth tergum (Fig. 141) with widely U-shaped emargination, without lobes but with scattering of submarginal setae; emar-



FIGS. 137-149, *Chionea valga*. 137, right antenna of male, approximately dorsal aspect (slide-mounted). 138, basal portion of left antenna, male from Michigan (J. S. Rogers slide 2848), showing subdivision of basal flagellomere. 139, thoracic dorsum of male, left lateral aspect, to show abrupt slope of mesonotum. 140, thorax of female, left lateral aspect; compare with *C. obtusa*, Figs. 123, 124. 141, ninth abdominal segment of male, dorsal aspect (left basistyle and dististyle omitted, tenth segment pushed inward to expose gonapophyses). 142, right gonapophysis and penis, male from Wisconsin, right lateral aspect. 143, gonapophyses and penis, male from New Hampshire, dorsal aspect. 144, gonapophyses, male from Minnesota, dorsal aspect. 145, left dististyle, male from Wisconsin, ventral aspect (somewhat foreshortened because of curvature). 146, left dististyle, ventromesal aspect. 147, terminal abdominal segments, female from Michigan, left lateral aspect. 148, ninth sternum and genital furca, female from Vermont, posteroventral aspect. 149, genital furca, left lateral aspect. Scales: a—137-138, 142-146, 148-149; b—139-141, 147.

gination so wide and shallow as to give impression of entire margin in certain aspects. Gonapophyses in dorsal aspect (Fig. 144) broad, nearly oval, narrowest at rounded apex, with upturned mesal and lateral margins producing central concavity; mesal margin noticeably thickened; in lateral aspect (Fig. 142) deeply keeled, posterior end of keel deepest. Apex of penis with two slender, elongate filaments (Fig. 143). Basistyles each with rounded, pilose posteromesal lobe; dististyles (Figs. 145, 146) dark reddish brown, with prominent, acute, blackened mesal tooth; ventral tooth absent. Proctiger (tenth segment) membranous, pale, evenly narrowed toward rounded apex, extending approximately to tips of gonapophyses.

Abdomen of female: Setae of terga and sterna pale, more dispersed over sclerites than in male. Eighth tergum (Fig. 147) expanded at sides to more than half length of seventh tergum, shorter dorsally, with darkened, transverse line or zone near mid-length and with three or four marginal setae. Hypovalves extending to about mid-length of cerci, with upper margin slightly sinuate, lower margin straight near base, then curved upward toward narrowly rounded apex. Arms of genital furca (Fig. 148) relatively thick at base, slender in apical half, often more strongly divergent basally than apically, with nearly angular deflection near mid-length; base with divergent apodemes; darkened median portion of bursa copulatrix adjacent to furca visible through membrane in posterior aspect (or in cleared, slide-mounted specimens). Mid-ventral portion of ninth sternum (Fig. 148) not strongly sclerotized, somewhat trapezoidal in shape. Cerci about 1.3-1.4 times length of hypovalves (measured from notch to tip), upturned and slightly widened beyond mid-length (Fig. 147), with sharply rounded or acute apex.

Types.—Holotype, female, labelled only "174. ♀" and "M.C.Z. Type 26398," in the Museum of Comparative Zoology, Harvard Univ. This pinned specimen is considerably shriveled, with the abdominal sclerites telescoped. A label near the specimen reads "*Chionea valga* Harris Type." Mr. Norman Woodley found a catalogue of Thaddeus Harris' collection in the archives of the Museum of Comparative Zoology, and after the number 174 the entry "Dublin, N. H., Mr. Leonard." He also found a list of specimens entitled "Insects for Mr. Say, from T. W. Harris," on page 20 of which the number 174 is followed by "*Chionea valga,* mi. Mss. N. Hamp. 4." The type, therefore, although recorded from Massachusetts (i.e., in "A Report on the Insects of Massachusetts"), is apparently one of an original series of four or more from New Hampshire. I am indebted to Mr. Woodley for this help.

Chionea aspera Walker was based upon three males and one female, one male of which I have selected as lectotype (Byers, 1963: 160). The synonymy of this name with *C. valga* has long been asserted (first by Osten Sacken, 1869: 168), and examination of the types of *aspera* satisfied me that this synonymy is correct.

Osten Sacken had, in fact, commented on the probable synonymy of *aspera* and *valga* some years prior to the 1869 publication mentioned. The Report on the Insects of Massachusetts, containing Harris' description of *C. valga,* had a second edition in 1852 and a third in 1862. In the third, the 1841 description was repeated and a woodcut of the insect was added (Fig. 260). The following footnote by Osten Sacken also appeared on p. 601: "Mr. Walker has described two American species of this singular genus; one of them, *Chionea aspera,* seems to be identical with Dr. Harris's *C. valga.* I do not undertake to decide which name should be preferred. Dr. Harris's has the priority, but the few words he mentions about his insect can hardly be called a description. . . ." The lectotype male of *aspera,* from "Hudson's

Bay," is missing the middle leg on both sides but is otherwise intact; it has four flagellomeres beyond the fusion segment.

Chionea gracilis Alexander was based upon a single male specimen, differentiated from *valga* by being smaller (3.9 mm long) and slender, without incrassate femora. In these characters, however, this individual falls easily within the limits of variation of *C. valga*. The holotype, mounted on a microscope slide, is badly shriveled and misshapen, but some of the essential taxonomic details can be seen. I judge this to be an extraordinarily teneral specimen, so callow that it appears to have been mounted without being first cleared, for the digestive system, Malpighian tubules, central nervous system, and muscles of body and appendages are still plainly visible. The gonapophyses and sclerotized portions of the internal genitalia indicate the identity of the specimen, even though both antennal flagella are missing, most of the body hairs have been broken off, and the ninth abdominal tergum is badly distorted.

Chionea noveboracensis Alexander was also described from one specimen, a small female (3.5 mm long), said to differ from *valga* in being gray instead of reddish. The holotype, originally returned to R. C. Shannon, the collector, has been lost so could not be examined by me. However, I have seen two males and a female in Dr. Alexander's collection, determined by him as probably being his species *noveboracensis*, and these are, without question, all *C. valga*. Grayish pruinosity or even grayish body color are often seen in *valga*, so I am inclined to discount that one stated difference between the two forms. It furthermore seems to me that if there were in New York, in an area of considerable entomological activity such as the type locality of *noveboracensis*, some other species than *valga* and *scita*, it would have turned up again during the many years since *noveboracensis* was described.

Chionea waughi Curran was said to be ". . . most closely allied to *C. valga* but is readily distinguished by the absence of a wide projection on the upper margin of the basal portion of the genitalia and the long antennal flagellum." Just what the "wide projection" is that is absent in *waughi* and present in *valga*, I cannot be sure; perhaps it is the margin of the ninth tergum, or possibly Curran was referring to the membranous tenth segment, which in the holotype of *waughi* has become shriveled, exposing the gonapophyses. The described antennal difference is non-existent, seven segments being a common number in *valga*. Curran described *waughi* from three males and a female. I have examined the male holotype, female allotype and one of the male paratypes and am confident that these are the same as *Chionea valga*.

Variation.—Size variation in this species has been described earlier in the section on external morphology of adults. Some individuals of *C. valga* may be twice as long as others of the same sex taken on the same day in the same habitat; but dimensions of the genital segments vary much less than those of body and legs.

Antennae with four flagellomeres beyond the fusion segment are found in 96% of individuals in a Minnesota population, with 4% having five slender flagellomeres. Among specimens from Montmorency Co., Michigan, in contrast, 42% have five segments beyond the conical fusion segment. In some other samples the two forms are about equally common. One specimen from Michigan has a very short flagellomere just beyond the fusion segment, then five others. Another shows the second flagellomere distinctly subdivided into five non-articulated annuli (Fig. 138, from slide no. 2848, Univ. of Michigan collection).

Due to twisting toward the sides, the gonapophyses may appear more acutely tipped (Fig. 143) than they normally are in dorsal aspect (Fig. 144). In slender males the gonapophyses are usually separated throughout their length, but when robust males are preserved their thick basistyles may push the tips of the gonopophyses together (Fig. 141).

The upper margins of the hypovalves of the ovipositor vary from slightly and evenly convex to sinuate (slightly convex near the base, then very shallowly concave before the apex). There is much variation in details of the shape of the genital furca, but the dark axis, the relatively thick, short arms and the bifurcate anterior end are constant.

Relationships.—In overall appearance as well as in numerous details, *C. valga* most closely resembles the western *C. obtusa*. The similarity includes the abundant, long, thin hairs of legs and body, the general shape of male gonapophyses and dististyles, the genital furca of the female, and antennal length. In eastern North America, east of the Rocky Mountains, *valga* requires only to be differentiated from *scita* and *stoneana*, with which it sometimes is found. This is an easy matter, for *valga* and *scita* differ conspicuously in color and antennal length, and *valga* has longer setae on the legs and two or three more flagellomeres than *stoneana*. But at least in the vicinity of Edmonton, Alberta, *valga* appears to reach the range of the closely related *obtusa*. Males of these two species may be differentiated by details of the gonapophyses (for example, the outer edges are thicker and more strongly upturned in *valga;* compare Figs. 143 and 117), and by the evenly and shallowly emarginate, virtually entire ninth tergum in *valga* (Fig. 141) contrasted with the distinctly notched tergum in *obtusa* (Fig. 118). The terminal filaments of the penis in *valga* are not present in *obtusa;* however, this characteristic is independent of others elsewhere in the genus, such as being present in *albertensis* but not *scita*.

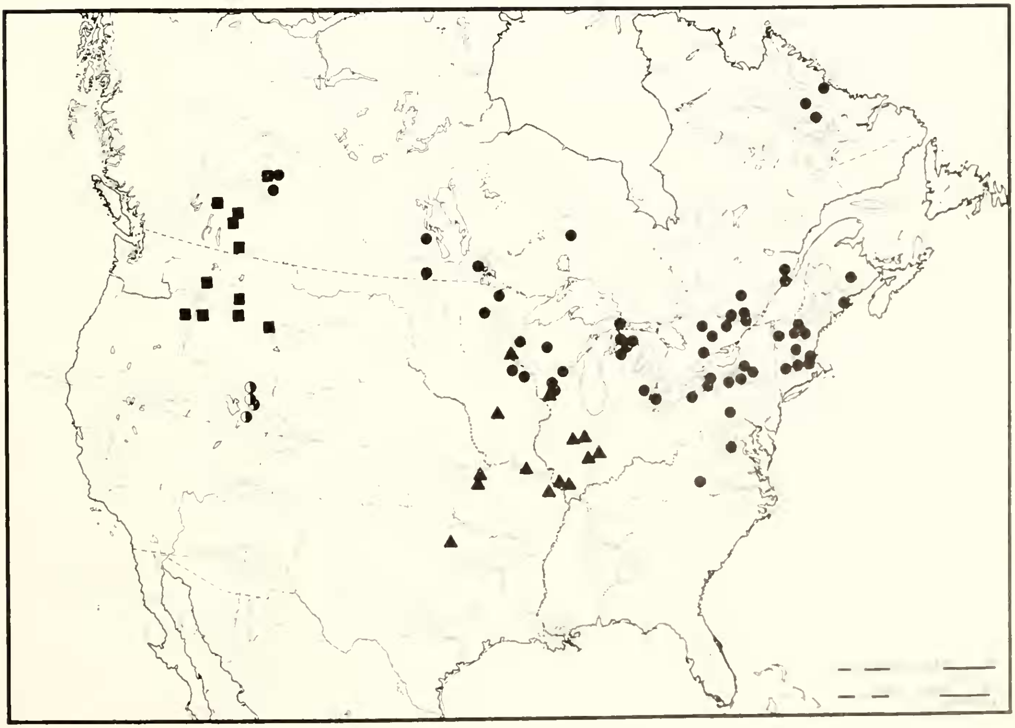
Females of *valga* are much easier to tell apart from those of *obtusa* than are males because of the conspicuous difference in their cerci (cf. Figs. 147 and 125) and to a lesser extent their hypovalves.

In both sexes the lateral profile of the mesonotum will serve to differentiate these species. The mesonotum is much more conspicuously "humped" in *valga* (Figs. 139, 140), its anterior surface nearly perpendicular to the pronotum. In *obtusa* the anterior slope of the mesonotum is much less abrupt (Figs. 123, 124). There are occasional individuals in which this difference is not as distinct as I have illustrated it; some robust males of *obtusa* approach the condition seen in *valga*, and some small, slender individuals of *valga* approach the *obtusa* profile. The described difference, however, is probably 98% reliable.

Geographic Distribution.—*Chionea valga* is the most widely distributed species in the genus, ranging from coastal Labrador westward to central Alberta and to Minnesota and southwestward along the Appalachian Mountains to southern Virginia (Map 3). This range spans 19 degrees of latitude and nearly 55 degrees of longitude and includes elevations from near sea level to about 925 m (3000 ft). Alexander (1942: 429) recorded the species from Saskatchewan; I have not seen specimens from that province but do not question the record, as *valga* extends westward into Alberta, where it apparently contacts the range of the very similar *C. obtusa*. It is a little surprising that there are so few records from Pennsylvania and Maine, particularly the former. I anticipate that *C. valga* will be found in southeastern Ohio, West Virginia, western Maryland, and further south in the Appalachian Mountains.

Seasonal Distribution.—There are collection records for every ten-day period from 10 November to 10 April, with numerous collections throughout December-March. At the northernmost locality, Voisey's Bay, Labrador (Newfoundland), *valga* is still present in early May. The September and October records, however, are not from particularly far-northern sites (Manitoba and New York). A conspicuous peak in the numbers of collections occurs in the last week of December, but this probably relates to the holiday season when many entomologists and other naturalists are away from school or work and into rural areas for skiing or the like. There is no evidence of more than a single generation per year; if there were two generations, their peaks might be obscured by the long individual life of the insects and by emergence delayed by unfavorable weather.

Habitats.—The broad range of *C. valga* includes a number of general types of habitat. Roughly from north to south these are: arctic tundra in coastal Labrador; subarctic spruce forest and more southern subarctic spruce-fir forest extending across much of southern Canada; white pine, jack pine and other evergreens in the northern Great Lakes region; and mixed hardwood forest of beech, maple, hemlock, birch, etc., from the upper Mississippi River eastward across Wisconsin, Michigan, New York, Pennsylvania and much of New England and extending southward along the crest of the Appalachian Mountains. Elsewhere the species penetrates to a limited extent the oak-hickory forest and the Appalanchian hardwood forest. The role of these major kinds of vegetation in the ecological distribution of *C. valga* is not clear, however. The range in general has fairly deep and persistent snow cover from November through March, with forest vegetation providing protection from wind and wind-blown snow as well as access to the snow surface. Nearly all specimens with habitat data were taken on snow or in pitfall traps of one sort or



MAP 3. Ranges of species of the *Chionea valga* group: *Chionea valga* (solid circles), *C. obtusa* (squares), *C. stoneana* (triangles) and *C. hybrida* (half-blackened circles). Each symbol represents one or more collections within a county (in the United States) or at a locality.

another; but two from Mifflin Co., Pennsylvania, were collected in a cave, in April.

Collection Records.—ALBERTA: Edmonton, 3 Dec. 1927 (1 ♀), 15 Dec. 1926 (1 ♂, 1 ♀), 29 Dec. 1926 (1 ♀), all collected by E. H. Strickland; Rimbey (32 mi NW of Red Deer, about 52°37′N, 114° 14′W), 22 Oct. 1929 (1 ♀). LABRADOR: Tessiuyakh Bay (56°14.9′N, 62°1.9′W), elevation 25 ft, on snow in mild weather, 5 May 1951, E. P. Wheeler (4 ♂); Voisey's Bay (same locality as Tessiuyakh Bay), on snow, 5 Dec. 1921, F. W. Waugh (3 ♂, holotype and paratypes of *C. waughi*); Cabot Lake (about 54°40′N, 64°20′W, labelled Labrador but actually in adjacent Quebec), Sept.-Oct. 1921, F. W. Waugh (1 ♀, allotype of *C. waughi*). MAINE: Washington Co., Woodland, 11 Jan. 1916 (1 ♂, 1 ♀); same, but 1 Dec. 1917 (1 ♂, 1 ♀); both collected by Olaf Nylander. MANITOBA: Aweme (20 mi SE of Brandon, about 49°37′N, 99°35′W), on boggy ground, ambient temperature "below zero," 12 Sept. 1910 (1 ♀); same locality, 27 Nov. 1917 (1 ♀), 12 Dec. 1924 (1 ♂); Dauphin vicinity (about 51°10′N, 100°00′W), March 1919, Mrs. Hippisley (1 ♂); Whiteshell, Red Rock Lake, 23 Feb. 1970, W. O. Pruitt (1 ♂, 1 ♀). MASSACHUSETTS: Berkshire Co., Monterey (labelled Monterrey), Jan. 1951, J. D. Miner (1 ♂); Essex Co., Andover, 1 Jan. 1874, F. C. S. (1 ♂); Hampshire Co., Amherst, 19 Feb. 1929 (1 ♂), 12 Dec. 1926 (1 ♂), Orient Springs, 3 Feb. 1929 (1 ♀), all collected by C. P. Alexander; Cummington, elevation 1400 ft, crawling on snow in snow storm, 2 Jan. 1932 (1 ♂); same locality, 5 Jan. 1946 (3 ♂, 3 ♀); same, on snow in open pasture, 1 Feb. 1946 (2 ♀); same locality, 20 Dec. 1932 (1 ♀); all collected by A. B. Gurney; Middlesex Co., Sherborn, 15 March 1925, C. A. Frost (1 ♂); Framingham, 19 Jan. 1917, C. A. Frost (1 ♂); Malden (1 specimen; see Johnson, 1912); Tyngsboro, 6 Dec. 1911, J. H. Emerton (1 ♂); same, no date, Blanchard collector (1 ♂, 1 ♀). MICHIGAN: Cheboygan Co., Reese's Bog (north shore Burt Lake), on surface of snow, 23 Feb. 1952, W. O. Pruitt (1 ♀); same, 24 Feb. 1952 (2 ♂); Chippewa Co., Chase Osborn Preserve, Sugar Island, on snow, air temperature 0°C, 20 Dec. 1949, W. O. Pruitt (1 ♂); Crawford Co., near Lovell's, 11 Jan. 1936, J. W. Leonard (1 ♂); Montmorency Co., Hunt Creek Station (a laboratory for fisheries studies), 13 Jan. 1942 (9 ♂, 5 ♀), 29 Jan. 1941 (1 ♀), 2 Feb. 1941 (2 ♂, 1 ♀), 5 Feb. 1942 (1 ♀), 6 Feb. 1942 (2 ♀), 12 March 1942 (1 ♀), 8 Dec. 1942 (3 ♂, 1 ♀), 31 Dec. 1941 (1 ♀), all collected by Justin W. Leonard; Oakland Co., Wixom, Proud Lake State Recreation Area, walking on snow in red pine woods, overcast, 8°C, near Huron River, 13 Jan. 1979, T. L. Heller (1 ♂); Presque Isle Co., Lake Huron (T37N, R2E, Sec. 14), on ice, 50 yards from shore, 23 Feb. 1952, Erna Pruitt (1 ♂); on ice on Palestri's Creek, 22 Feb. 1952, Erna Pruitt (1 ♂). MINNESOTA: Clearwater Co., Itasca State Park, 22 March 1979 (2 ♀); Dakota Co., in pit traps (baited with 4% formalin or 50% wine) under 12-19 cm snow, 6-18 Jan. 1972, Owen Marshall (13 ♂, 5 ♀); same, but 18 Jan.-1 Feb. 1972, snow 12-36 cm deep (1 ♂, 6 ♀); same, but 8-15 Feb. 1972, snow 17-33 cm deep (1 ♂, 2 ♀); Koochiching Co., Big Falls, 26 March 1971 (1 ♀); Olmstead Co., Rochester, on snow 1 ft deep, 15°F, 25 Dec. 1905 (1 ♂); same, 27 Dec. 1905 (1 ♂, 1 ♀) (not seen; both reported by Ainslie, 1906). NEW BRUNSWICK: Fredericton, 21 Dec. 1929 (1 ♂); York Co., Hanwell Road, on snow, 1 Feb. 1970 (1 ♀). NEW HAMPSHIRE: Carroll Co., Jackson, on snow 2-3 ft deep, in sheltered places at edge of woods, 20 Feb. 1907, J. H. Emerton (3 ♂, 1 ♀); Cheshire Co., Jaffrey, 4 March (1 ♀); Coos Co., Jefferson, 23 Feb. 1970, O. S. Flint, Jr. (4 ♂, 2 ♀); Mt. Clinton (2 mi NE of Crawford House, Crawford Notch), in forest, 45°F, 30 Jan. 1970, S. Peck (1 ♂);

White Mts., on snow, Jan. 1969, S. Peck (2 ♂); Grafton Co., Mt. Lafayette, 8 mi N of Lincoln, 3000 ft, on deep snow, 18 Jan. 1969, S. Peck (1 ♂); Hanover and vicinity, 31 Dec. 1960 (1 ♂, 1 ♀), 8 Jan. 1961 (1 ♀), 26 Dec. 1961 (1 ♀), 23 Dec. 1962 (2 ♂, 1 ♀), 31 Dec. 1962 (1 ♂), 5 Jan. 1963 (2 ♀), 24 Dec. 1963 (2 ♂, 1 ♀), all collected by K. W. Cooper. NEW YORK: Cattaraugus Co., Otto, 18 March 1896, J. H. Comstock (1 ♀); Chenango Co., Bainbridge, 15 Dec. 1922, L. J. W. Jones (1 ♂); Erie Co., Lancaster, no date, M. C. Van Duzee (1 ♂); Onondaga Co., Manlius, 1 Oct. 1872 (1 specimen, not seen; see Needham, 1908: 207); Steuben Co., Lake Keuka, Dec. 1905 (1 ♂, 1 ♀); Tompkins Co., Buttermilk Falls State Park, on snow, 29 Dec. 1966 (2 ♂); Enfield Glen (Enfield Falls), 21 Feb. 1920, S. Emerson (1 ♂); Coy Glen, elevation 800 ft, 25 Feb. 1917, R. C. Shannon (1 ♀, type of *C. noveboracensis*, not seen); Ithaca, 15 Dec. 1907 (1 ♂, type of *C. gracilis;* published collection date 21 Dec. 1914); also the following reported from Tompkins Co. by Needham (1908: 207) but specimens not seen: Ithaca, 15 March 1896 and 15 Nov. 1892, Forest Home, Dec. 1907. ONTARIO: Carleton Co., Ottawa, on snow, 23 Dec. 1924, G. H. Hammond (1 ♀); Essex Co., 1 Jan. 1936, C. A. Neil (1 ♀); Nipissing Co., Algonquin Park, 29 Dec. 1951, F. P. Ide (3 ♂, 2 ♀); Hastings Co., Graphite Lake, near Maynooth, on snow, 18 Nov. 1967, J. E. H. Martin (1 ♀); Ontario Co., 1 Feb. 1941, F. A. Urquhart (3 ♂, 5 ♀); Renfrew Co., Arnprior, temperature 20°F, 11 Jan. 1920, C. Macnamara (1 ♂, 1 ♀); same locality, 13 Feb. 1920 (1 ♂); Thunder Bay District, St. Martin's Falls, Albany River, no date (3 ♂, 1 ♀, types of *C. aspera*); York Co., Humber River, 13 Jan. 1952, F. P. Ide (1 ♀). PENNSYLVANIA: Erie Co., Edinboro, Conneauttee Creek tributary, 1465 ft, in emergence trap, on snow, –4°C, 18 Feb. 1980, Becky Travis (1 ♀); same locality, 15 Jan. 1981, B. Travis (1 ♂); Mifflin Co., Aitken Cave, 4 April 1937, K. Dearolf (1 ♂, 1 ♀). QUEBEC: Gatineau Co., Aylmer (7 mi SW of Hull), on snow, 20 and 24 Dec. 1938 (2 ♂); Gatineau National Park, near Hull, Lake Phillip, on snow, 29°F, 29 Nov. 1970, S. Peck (1 ♀); Camp Fortune, at Old Chelsea (6 mi NW of Hull), on snow, 18 Feb. 1951 (1 ♂) and 4 March 1951 (1 ♂); Old Chelsea, 22 Jan. 1967, D. M. Wood (2 ♀); Gatineau Park, near Old Chelsea, 22 March 1970, L. Masner (1 ♀); Lac Roddick, 16 mi S of Maniwaki, on snow, 24 Feb. 1980, L. Harner (1 ♂); Quebec, Mont Ste. Anne, 12 Mar. 1978, J. R. Vockeroth (2 ♂, 3 ♀); Laurentide Prov. Park, Camp Mercier, 36 mi N of Quebec, 23 Feb. 1975, F. Brodo (10 ♂, 6 ♀); Indian House Lake (56°08′N, 64°44′W), elevation 1000 ft, 22 Nov. 1944, R. C. Clement (specimens not seen). VERMONT: Chittenden Co., 3 mi N of Bolton (Middle Bryant Lodge), elevation above 2000 ft, on deep snow in yellow birch woods, 23 Jan. 1955, Rodger Mitchell (26 ♂, 19 ♀). VIRGINIA: Giles Co., Cascades Trail (near Pembroke), in fine, loose litter in hollowed base of tree, about 2 in snow on ground, 7 Jan. 1981, J. A. Vaughan (1 ♂); Warren Co., Shenandoah National Park, Dickey Ridge (north end of Park), on snow, 17 Feb. 1970, O. S. Flint, Jr. (1 ♀). WISCONSIN: Burnett Co., 11 mi E, 4 mi S of Siren, on snow, 1 Feb. 1970, D. Hansen (1 ♂, 1 ♀); Iowa Co., Clyde Twp., Sect. 12, on snow, north-facing slope, Dec. 1967 (1 ♂); Price Co., walking on snow, 21 Jan. 1979 (1 ♂, 2 ♀); Sauk Co., Otter Creek, on snow along stream bank, 8 Feb. 1969, R. P. Narf (1 ♀); same, but 7 Jan. 1967 (1 ♂); same, but 27 March 1967 (1 ♀); Parfrey's Glen, T11N, R7E, Sect. 25, 7 Jan. 1967, R. P. Narf (3 ♀); same, but Sect. 22-23, 13 March 1965 (1 ♀); same, but 14 March 1965, J. K. Lawton (1 ♀); Waushara Co., Bird Creek, T18N, R10E, Sect. 3, Hwy. 21 bridge, 9 Feb. 1967 (1 ♀).

The C. alexandriana Group

A western montane group of species. Body color brown, with evident pattern on abdominal terga in some species, dark brown or black; antennae with two to four flagellomeres beyond fusion segment; gonapophyses of male with upturned, often hook-like apical point, usually broad at base and conspicuously narrowed toward apex, in dorsal aspect; eighth abdominal tergum of female short, much less than half length of seventh tergum; median portion of ninth sternum a sclerotized plate, often with three posterior lobes or teeth. Included species: *alexandriana* Garrett, *carolus* Byers, *durbini* new species, *excavata* new species, *jellisoni* new species, *lyrata* new species and *nigra* new species.

Chionea alexandriana Garrett

Chionea alexandriana Garrett, 1922: 62-64, Figs. 6-11; Alexander, 1965: 72.

As *Chionea valga*: Treherne, 1920: 201-202 (misidentification).

Diagnosis.—A dark brown, western, primarily montane species; antennae with three to four flagellomeres; male gonapophyses slender and hooked at apex, dististyles smoothly rounded dorsally; female cerci slender, upturned in distal half, noticeably longer than hypovalves.

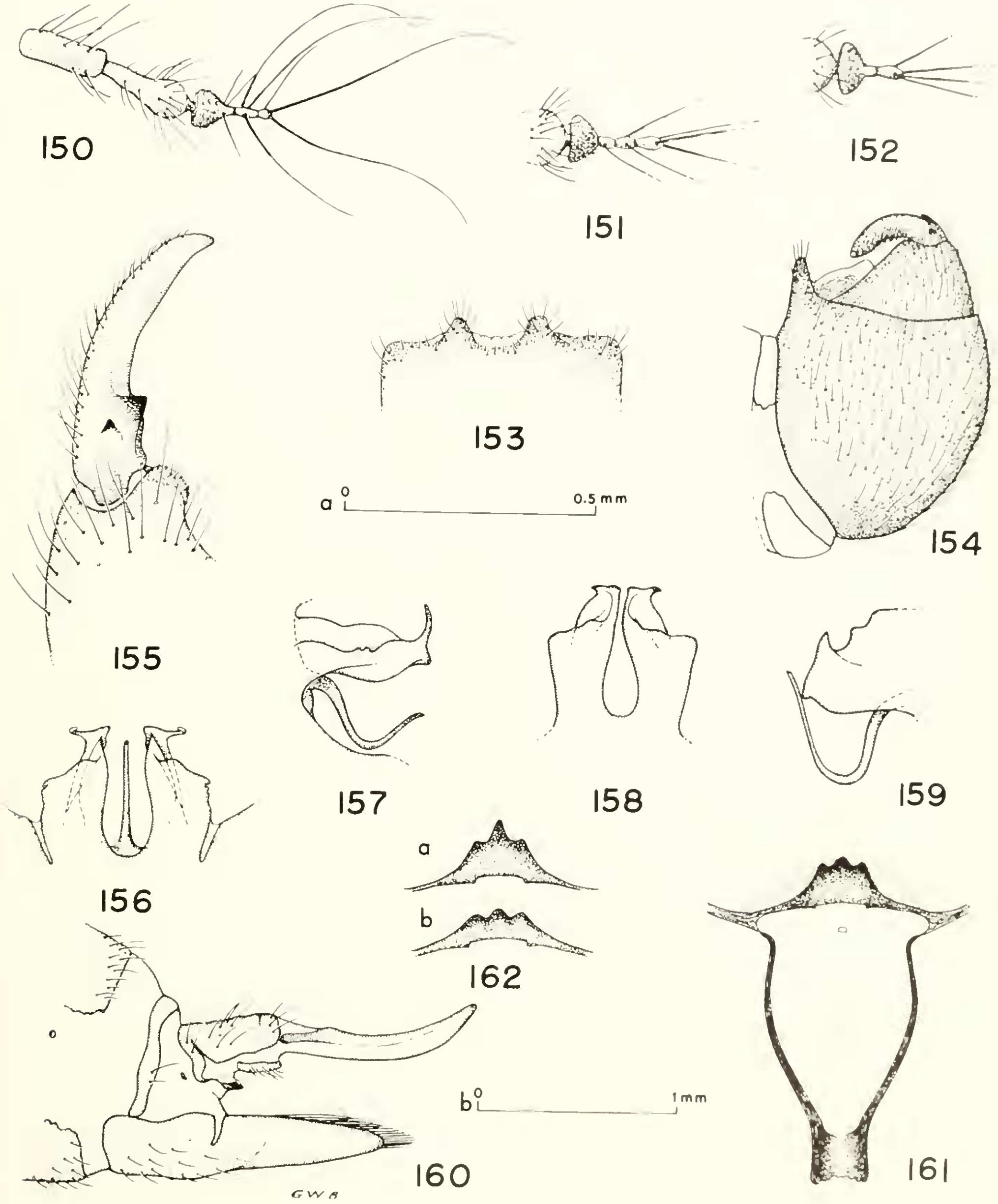
Description.—General appearance: Head dark grayish brown, thorax dark brown; abdominal sclerites light brown to brown, terga darker brown anteriorly, along midline and at lateral edges; ninth segment of male dark grayish brown, cerci of female amber-brown; pleural membranes grayish tan. Length of male about 4-8.3 mm, female about 4-8 mm, exclusive of antennae.

Head: Antennae (Figs. 150-152) comprising scape, pedicel, and usually three, not uncommonly four flagellomeres; fusion segment short, turbinate to subconical, its apical portion sometimes resembling an additional short segment. Eyes with about 110-120 ommatidia each.

Thorax: Halteres pale grayish brown (in alcohol) to yellowish brown (dried), contrasting with color of thoracic dorsum. Legs dark brown to dark reddish brown; seven (4 dorsal, 3 ventral) to 11 longitudinal rows of setae on femora, in males sometimes additional hairs not in rows; second and succeeding tarsomeres blackish brown to black.

Abdomen of male: Posterodorsal edge of ninth tergum (Fig. 153) with a broad, shallow median emargination; a small, thick lobe bearing six to eight setae at each side of emargination. Gonapophyses (Figs. 156-159) broad at base, narrowing abruptly near mid-length; apical portion hook-like, with prominent, angular ventral process, slender, curved upward to acute tip; space between gonapophyses narrowly U-shaped, or slightly narrowed caudally, less often constricted near posterior end; apex of penis unmodified. Basistyles moderately thick for genus to thick in large males; posteromesal lobe of each pilose, sometimes with two rounded protuberances. Dististyles (Fig. 155) dark brown, thick, with prominent, blackened, subacute mesal tooth at base, then abruptly narrowed, more or less circular in cross-section, and evenly tapered to apex; ventral tooth usually small, in some large males darkly sclerotized but not strongly developed. Tenth segment broad at base, narrowed near mid-length, pigmented and lightly sclerotized laterally.

Abdomen of female: Eighth tergum short (i.e., slender) throughout. Hypovalves of eighth sternum comparatively slender, dorsal margin sloping downward toward apex, ventral margin curving upward, producing subacute apex. Arms of genital furca slender apically, slightly thickened near base (Fig. 161); basal portion about as wide as long, weakly sclerotized medially. Mid-ventral portion of ninth sternum (Figs. 161, 162a,b) well



Figs. 150-162, *Chionea alexandriana.* 150, left antenna of male, mesal aspect. 151, 152, antennal flagella of females from Alberta, showing variation in number of flagellomeres (in 152, one of the four setae arises on the fusion segment). 153, ninth abdominal tergum, male, dorsal aspect. 154, genital segment of robust male, left lateral aspect. 155, left dististyle, ventral aspect. 156, gonapophyses and penis, dorsal aspect. 157, same, left lateral aspect. 158, 159, gonapophyses of atypical male from ice cave in Oregon. 160, terminal abdominal segments, female, left lateral aspect. 161, ninth sternum and genital furca, female, ventral aspect. 162a, b, variations in median portion of ninth abdominal sternum. Scales: a—150-153, 156-159, 161-162; b—154-155, 160.

sclerotized, with three blunt teeth, middle one longest; a rounded, lightly sclerotized area above and to each side of darkened portion. Cerci elongate, about 6-6.5 times as long as greatest width, curved upward in apical half, noticeably longer than hypovalves (about 1.2-1.4 times as long as hypovalve measured from notch to tip).

Garrett's (1922: 63) illustrations do not adequately portray the structural details he intended to show; they are, in fact, rather grotesque caricatures.

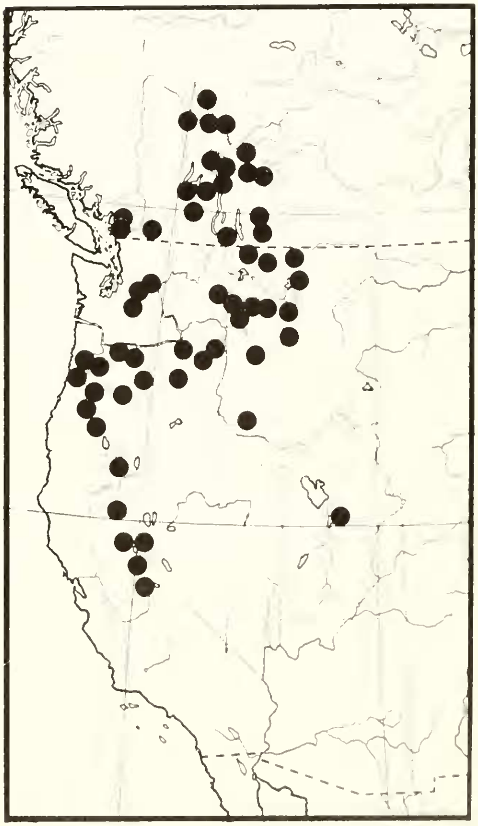
Types.—Holotype, male, Cranbrook, British Columbia, elevation 3500 ft, 22 February 1921, C. B. D. Garrett collector. Allotype, female, and two female paratypes, same data as holotype. Additional paratypes: 1 ♀, type locality but collected 13 February 1920; 1 ♀, Canal Flats, Kootenay Valley, British Columbia, March or April 1921. Holotype, allotype and Kootenay Valley paratype in collection of Mr. C. B. D. Garrett, Cranbrook, British Columbia. One paratype each sent to Dr. C. P. Alexander, Amherst, Massachusetts, United States National Museum, Washington, D.C., and Canadian National Collection (Canada Department of Agriculture), Ottawa, Ontario.

Variation.—In a series of 15 males and 17 females from the type locality, ten males and ten females had two flagellar segments beyond the fusion segment, and five males and seven females had three. In individuals from other localities, also, the number most often seen is two in addition to the fusion segment. Rarely, there is only one (Fig. 152). Variation in the number of rows of femoral setae, in the ventral tooth of the male dististyle, and certain other characters has already been noted. The lobes of the ninth tergum of the male vary from low and broad to prominent and longer than wide. Seen from above, the space between the gonapophyses may be narrowly U-shaped or a little constricted near the bases of the apical hooks. A single male in a collection of 18 individuals from an ice cave in Union Co., Oregon, has this space strongly constricted caudally (Fig. 158); the gonapophyses are atypical in other respects as well (Fig. 159), with relatively short, thick apical hooks. Compression by the basistyles during preservation may distort the gonapophyses by partial rotation to the sides or constriction of the space between them. The outline of the gonapophyses (in this and all other species) can also be made to vary by compression on a microscope slide, but this kind of distortion should not in interpreted as variation. In the genital furca of the female the deflected apices of the arms vary in the degree of sclerotization and may not be as dark as shown in the illustration. There is considerable variation also in the relative sizes—particularly the lengths—of the three teeth of the ninth sternum (cf. Figs. 161, 162).

Relationships.—The gonapophyses and antennae of the male and the combination of short eighth tergum and abbreviated antennae in the female show the close relationship of *Chionea alexandriana* with *nigra* and *jellisoni*, and suggest relationship with *excavata* and *lyrata* and a somewhat more distant relationship with *carolus* and *durbini*. This grouping of species (the *alexandriana* group) is reinforced by several other similarities, such as the structure of the ninth sternum in the female and the internal reproductive systems of both sexes. Within the group, *alexandriana* most closely resembles *C. nigra* n. sp., from which it differs most conspicuously in color. These two species may also be differentiated by the more prominent ventral process on the apical hook of the male gonapophysis and by the tridentate ninth sternum in the female of *alexandriana*. These is a difference—though not always apparent—in the shape of the fusion segment of the antenna, longer in *alexandriana*, short and broadly turbinate in *nigra*.

Geographic Distribution.—Chionea alexandriana has been found from the mountains of western Alberta and southern British Columbia southward through Washington, Oregon, Idaho and western Montana, to the east of the Great Basin in the Wasatch Mountains of Utah and along the Sierra Nevada to western Nevada and east-central California. Only recently (1981) has this range been extended significantly northwestward, to the vicinity of Whitehorse, Yukon Territory, over 800 miles from the nearest known localities in southwestern Canada. (This locality is not included on the distribution map, Map 4). The species is generally montane, but occurs from near sea level to 3000 meters (9800 ft). It coexists with several other western species, both in its general range and in its particular habitats. It is the most widely distributed of the western group of species (Map 4).

Seasonal Distribution.—There are collection records from some part of the range for every ten-day period from 1 October through 20 April, with isolated collections in mid-September and mid-May. Concentrated local collections, such as those made by Garrett and Woods in British Columbia and Chapman in Montana, show a peak period of abundance of the adults in November and December and an almost equally large but more prolonged peak in February and March. There may be two generations per year. As for some other species, the largest number of separate collections is in late December and early January, probably as a result of academic holidays. The snow cover was sometimes fresh, other times older and firm, and varied from 2.5-3 ft in thickness. Temperatures recorded at times of collection ranged from 21-32°F. Although active at 22°F and slightly so at 21°F, *C. alexandriana* was in cold stupor at 19.5°F (Chapman, 1954: 362). Near Mara in the northern Okanagan Valley, British Columbia, Mr. H. J. Blurton, a trapper, observed *Chionea alexandriana* on the snow in open stands of spruce and balsam (but not in dense stands) near timberline, between 5000 and 6500 ft. He saw the insects occasionally during January through April and noted that they were active on the snow surface on stormy days in April but were not seen when the temperature was so high as to make the surface moist (Treherne, 1920). Data from many collectors are less complete and do not indicate whether the specimens were taken on snow or not; probably most were, as *Chionea* is ordinarily not otherwise likely to be seen. However, in the Lava Beds National Monument, Modoc Co., California, Mr. Joe Schuh collected a male of *alexandriana* from an abandoned nest of a pack rat (*Neotoma* sp.). Occurrence



Map 4. Range of *Chionea alexandriana*. Each spot represents one or more collections within a county (in the United States) or at a locality. A locality near Whitehorse, Yukon Territory, is not indicated on the map.

of *alexandriana* in an ice cave has been mentioned earlier.

Habitats.—The clearest picture of the ecological distribution of *Chionea alexandriana* comes from the studies of winter insects made in the Bitterroot Mountains in Missoula Co., Montana, by Dr. John A. Chapman (1954). He found the flies always on snow and invariably in forested areas, although sometimes several yards from the nearest tree. Chapman's collections were made at elevations from 3600-8000 ft, most of the flies being taken between 6000 and 7000 ft. The forest at these elevations is composed largely of lodgepole pine (*Pinus contorta*) and Douglas fir (*Pseudotsuga taxifolia*).

Collection Records.—ALBERTA: Banff National Park, Boulder Pass, 7490 ft, on 12 in of snow, 14 Oct. 1968, K. W. Richards (2♂, 1♀); Banff National Park, Castle Mountain (Mt. Eisenhower), on snow, 5400 ft, 0°F, sunny, 31 Jan. 1956 (2♂); Banff vicinity, 20 March 1930, Owen Bryant (1♂); same, but 15 April 1928 (1♂, 1♀); same, but on snow, 23 Oct. 1932 (1♂); same, but Cascade Mountain, 6000 ft, 26 Jan. 1928 (1♀); also, a few specimens without date or collector's name from vicinity of Banff; Jasper National Park, Twp. 43, Range 1, 6200 ft, Sta. 7, 2-4 Oct. 1964 (3♂, 4♀); same, but 7600 ft, Sta. 8 (2♀); Athabasca Glacier area, 13 Oct. 1970, G. G. E. Scudder (3♂, 1♀); W of Ya-Ha Tinda Ranch (about 20 mi N of Banff), 27 Jan. 1960 (5♂, 6♀, including 1 mating pair). BRITISH COLUMBIA: Cranbrook (49°31′N, 115°46′W), elevation about 3000 ft, on snow, 1 Nov. (2♂, 1♀), 2 Nov. (1♂), 4 Nov. (3♀), 10 Nov. (1♂), 14 Nov. (1♀), 17 Nov. (4♂, 3♀), 21 Nov. (1♀), 23 Nov. (1♂), 3 Dec. (1♀), 13 Feb. (1♀), 22 Feb. (1♂, 3♀, types), 15 March (3♂), 16 March (1♂, 2♀), 12 April (4♂, 2♀), 19 April (4♀), all collected by C. B. D. Garrett, with no years recorded; Glacier National Park, 7 Dec. 1979 (1♂), 24 Dec. 1979 (5♂, 3♀), 13 Feb. 1977 (1♂, 1♀), 20 Feb. 1980 (1♂, 2♀), 24 Feb. 1979 (4♂, 3♀), 16 March 1980 (4♂, 5♀), all collected by John G. Woods; Goldstream River, 118°45′W, 52°45′N, 26 Dec. 1979 (11♂, 9♀), John G. Woods; Hunter's Range, E of Mara (50°41′N, 118°45′W), elevation 5000-6500 ft, on snow, Feb. 1927 (4♀), March 1920, H. J. Blurton (4♂, 2♀, including a mating pair); Kootenay Valley, March-April 1921 (1♀); Manning Prov. Park, near 0°C, snowing heavily, 5000-5700 ft, 10 Feb. 1979 (4♂, 3♀); same locality, near 0°C, on deep snow, 4000 ft, 11 Feb. 1978 (1♂); same, Cambie Creek, –1°C, about 4300 ft, 16 Mar. 1980 (3♂, 7♀); same –8°C, 17 Feb. 1980 (1♂); same but about 0°C, after sunset, 4500-5800 ft, 16 Feb. 1980 (5♂, 8♀); same but –5 to +5°C, in dappled shade or bright sun, on snow, 28 Feb. 1981 (6♂, 6♀); all collected by S. G. Cannings; Manning Park, in shade on snow, 4000 ft, 3°C, 1 Mar. 1981, L. Vasington (1♂); same but on snow at dusk, about 0°C, 4000 ft, 9 Feb. 1980, R. J. Cannings (1♂); Garibaldi Prov. Park, Diamond Head Trail, about 4000 ft, –1 to 3°C, overcast, 5 Apr. 1981, S. G. Cannings (1♀); Mount Revelstoke National Park, 28 Nov. 1976 (1♀), 12 Dec. 1979 (1♀), 25 Dec. 1979 (1♀), 28 Dec. 1976 (1♂, 1♀), 13 Jan. 1980 (2♂, 5♀), 1 Feb. 1977 (1♀), 3 Feb. 1980 (1♀), 9 Feb. 1980 (2♂, 3♀), 10 Feb. 1980 (8♂, 6♀), 23 Feb. 1978 (1♂, 1♀), all collected by John G. Woods; Salmon Arm (50°39′N, 119°16′W), 2 Jan. 1926 ("1-2-1926") (2♂); Silver Star Prov. Park, Silver Star Mt., on snow in sunshine, noon, 12 Jan. 1981, A. Bryan (1♂, 1♀); same but snowing lightly, near –3°C, 1100-1300 hrs, 29 Jan. 1981, A. Bryan (1♂, 4♀); Vancouver, on snow, 21 Jan. 1933, H. B. Leech (1♀); Vancouver vicinity, Hollyburn Mt., 1300 ft, on snow, 1 Apr. 1978, P. Withler (1♂); same but 4000 ft, on snow, –3°C, 1 Mar. 1979, S. G. Cannings (1♀); Crown Mt., 3 Nov. 1935, J. Poole

(1 ♂, 1 ♀); Mt. Seymour (15 mi NE Vancouver), 1000 m, overcast, snowing, 18 March 1980, A. Grass (1 ♀); Wells Gray Provincial Park (about 50°30′N, 120°00′W), along willow flats, Stillwater, 1 Jan. 1962, P. Joslin (1 ♀); same area, on snow, 27 Jan. 1981, T. Goward (2 ♀); Yoho National Park, fir-pine habitat, Lake O'Hara, 12 Feb. 1977, C. W. Aitchison (1 ♂, 1 ♀); Yoho Park, 6 Feb. 1977 (1 ♀), 25 Feb. 1980 (1 ♀), both John G. Woods; Apex Mountain, Similkameen Dist., 6500 ft, on snow, 22 Dec. 1977, R. A. Cannings (1 ♀); Vaseux Lake, Okanagan River, 1900-2500 ft, on snow, 0-3°C, 23 Dec. 1980, R. J. Cannings (2 ♂); Mineral King Mine, 4500 ft, Toby Creek, near Lake Windermere, snowing, −1 to 0°C, coniferous forest, 8 Feb. 1960, G. O. M. Stewart (4 ♂); Whistler Mountain, 5000 ft, 10 Oct. 1970, I. Britt (1 ♀); Paul Ridge, 5000 ft, shady N slope, 0-1°C, 11 Jan. 1981, S. G. Cannings (1 ♀). CALIFORNIA: Alpine Co., Carson Pass, off Calif. Hwy. 88, 8600 ft, collected dead on snow 3-4 ft deep, 15 Dec. 1974, D. Durbin (1 ♂); Modoc Co., Lava Beds National Monument, Crystal Cave, in nest of dead pack rat, 9 Feb. 1962, J. Schuh and E. Hansen (1 ♂); Mono Co., Carnegie Inst. Exper. Sta., 9800 ft, on snow, 28 Oct. 1973, D. Durbin (1 ♂); Nevada Co., Sagehen Creek at Univ. Calif. Field Station, 16 March 1972, R. A. Haick (1 ♂); Plumas Co., near Caribou, 24 Jan. 1922, H. S. Barber (1 ♀). IDAHO: Benewah Co., Crystal Creek, on snow, 22 Dec. 1968, M. M. Furniss (2 ♂, 3 ♀); Boise Co., 0.25 mi E of Idaho City, on snow in pine forest, 7 Dec. 1974, G. A. Shook (1 ♀); Boundary Co., Round Prairie, 2-3 mi W of Addie on U.S. Hwy. 95, Hall Mt., walking on snow on old logging trail in mixed coniferous forest, in light rain, about 35°F, 11 Nov. 1973, A. Greene (1 ♂); Clearwater Co., East Fork of Potlatch River, 5.5 mi E of Bovill, on snow, 11 Dec. 1978, R. C. Biggam, T. F. Hansen and P. C. Schroeder (3 ♂, 1 ♀); Idaho Co., Clearwater National Forest, Mud Creek Jct., 25 Nov. 1978, R. C. Biggam and M. A. Maurer (1 ♂); Warm Springs Creek, about 20 mi SW of Lolo Pass, on U.S. Hwy. 12, 28 Dec. 1975, A. Greene (4 ♂, 2 ♀); Latah Co., 4 mi NE of Harvard, Lost Creek, on snow, 6 Dec. 1975, R. C. Biggam (1 ♀); 3 mi S of Helmer, Little Boulder Camp, 4 Dec. 1971, W. J. Turner (1 ♂, 2 ♀); 6-7 mi NW of Troy, along Big Meadow Creek, overcast, still, 20°F, 14 Dec. 1975, A. Greene (1 ♂); Big Meadows Rec. Area, 4.5 mi NNW of Troy, 9 Dec. 1973, M. C. Hunter (3 ♂); 4 mi E of Emida Summit, Alt. Hwy. 95, 11 Feb. 1978, D. M. Kirkbride (1 ♂, 1 ♀); Shoshone Co., Clarkia, on snow, 14 Dec. 1960, W. F. Barr (1 ♂); Gold Hill, on St. Joe Divide, S of Wallace, on snow, 6000 ft, 23 March 1957, D. Fellin (1 ♂). MONTANA: Glacier National Park, near foot of Lake McDonald, walking on snow, near 22 F, 31 Dec. 1966 (1 ♀); Lake Co., Lion Creek, Swan Valley, 4 March 1972, R. A. Haick (1 ♀); Lincoln Co., Leigh Lake, 20 mi S of Libby, 5200-5400 ft, on fresh snow on rocky ground with moss, bear grass and sparse shrubs, 17 Sept. 1976, L. Wright (1 ♂, 2 ♀); Mineral Co., St. Regis, on snow, 28 Dec. 1957, H. R. Dodge (3 ♂, 2 ♀); Missoula Co., Lolo vicinity, Bitterroot Mountains, on snow, 6000-7500 ft, 14 Feb. 1953 (14 ♂, 12 ♀, including 2 mating pairs); same, but 3800 ft (1 ♂, 1 ♀); near Lolo, on fresh snow, about 6500 ft, 14 March 1953 (2 ♂, 1 ♀); same, but 6700 ft (1 ♂, 1 ♀); Lolo, on fresh snow, Nov. 1950 (1 ♂, 1 ♀); near Lolo, on fresh snow, about 6500 ft, 8 Apr 1953 (7 ♂, 6 ♀); same, but 7800 ft, 16 May 1953 (1 ♂, 1 ♀); Missoula vicinity, on snow, 6 Feb. 1953 (2 ♂); same, but about 3600 ft, 9 March 1952 (1 ♂); same, but about 32°F, 21 Dec. 1952 (3 ♂); all collected by J. A. Chapman; Missoula Co., on snow 26 Feb. 1957, H. R. Dodge (1 ♂, 1 ♀); Elk Creek, Lubrecht Forest, 4000 ft, 22 Jan. 1972,

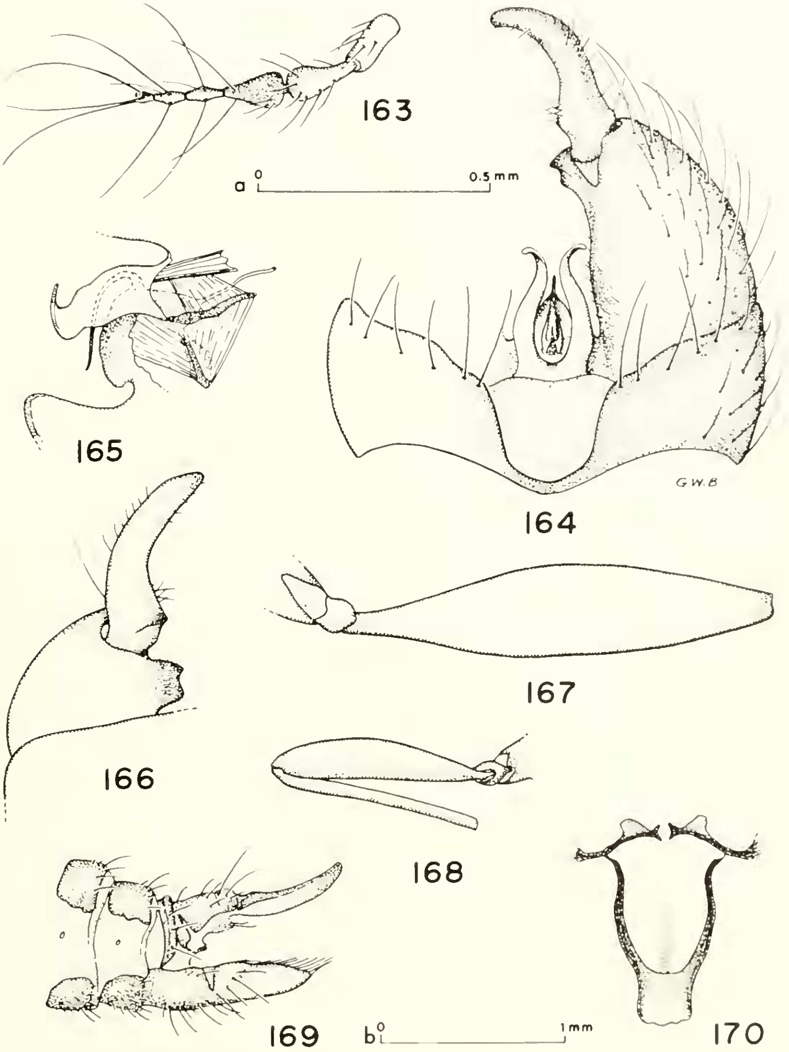
R. A. Haick, D. D. Jones and A. L. Costa (3 ♂, 7 ♀); Grant Creek, GC-3, 13 Feb. 1972, R. A. Haick (2 ♂, 1 ♀); Grant Creek, 13 Dec. 1971, R. A. Haick (1 ♂); Butler Creek, Snow Bowl, 15 Apr. 1972, R. A. Haick (1 ♀); Ravalli Co., Tin Cup Canyon, 3 mi W of Darby, on snow, near 4100 ft, 29 Nov. 1972 (2 ♂, 1 ♀); same, but 1 Dec. 1970 (2 ♂); same, but 13 Dec. 1973 (5 ♂, 2 ♀); same, but 16 Jan. 1972 (2 ♂, 1 ♀); all collected by W. L. Jellison: Lake Como, on snow, 31 Dec. 1969 (1 ♂); same, but 27 Nov. 1965 (1 ♀); Gird's Creek, vermiculite mines, on snow, 15 Oct. 1954 (1 ♂); all collected by W. L. Jellison; Tin Cup Canyon, 3 mi W of Darby, 4100 ft, on snow, 1 Jan. 1971, G. W. Byers (1 ♂, 1 ♀); West Fork Ranger Station, on snow, 28 Nov. 1962, W. L. Jellison (2 ♂, 1 ♀). NEVADA: Washoe Co., NE of Hunter Lake, Mt. Rose, 7200-8200 ft, 19 Jan. 1923, H. S. Barber (4 ♂). OREGON: Benton Co., Mary's Peak, Woods Creek Road, 7 March 1976, G. L. Peters (1 ♀); Clackamas Co., Mt. Hood, on snow, 32°F, 2 Jan. 1976, J. D. Lattin (1 ♀); Deschutes Co., Mt. Bachelor, on snow, 10°C, overcast, 26 Dec. 1980, L. Russell (2 ♀); same, 8000 ft, on snow, 3 Jan. 1969, K. Goeden (4 ♂, 8 ♀); 22 mi SW of Bend, near Todd Lake, 6300 ft, 21 March 1973, P. Lattin (1 ♀); Grant Co., Anthony Lakes Ski Area, on snow, 18 Feb. 1974, K. Goeden (7 ♂, 13 ♀); Hood River Co., 30 mi S of Hood River, 3 mi E of Bennett Pass, 20 Jan. 1974, P. Johnson (1 ♂, 3 ♀); Jefferson Co., Square Lake Trail, 1.5 mi E of Santiam Pass summit, on snow, 28 Dec. 1975, G. L. Peters (1 ♂); Klamath Co., Crater Lake National Park, on snow, park headquarters area, near 6500 ft, 15 Dec. 1957, D. H. Huntzinger (1 ♂); same, but 11 Feb. 1958, R. M. Brown (1 ♂); Lane Co., Pengra Pass, 22 mi SE of Oakridge, 5100 ft, 4 Jan. 1975, J. D. Lattin (1 ♂); Linn Co., McKenzie Pass, 5100 ft, 28 Dec. 1977, R. S. Zack (4 ♂, 4 ♀); 24 mi NW of Sisters, 4600 ft, 30 Dec. 1974, J. D. Lattin (3 ♂, 1 ♀); Lost Prairie, Willamette National Forest, on snow, 11 Jan. 1975, G. L. Peters (2 ♂, 1 ♀); 2 mi E of jct. of Oregon Hwys. 20 and 26, on snow, 18 Jan. 1975, D. C. Carlson (1 ♂, 1 ♀); Parish Lake Road, 6 mi S of Marion Forks, 3500 ft, 27 Jan. 1973, J. D. Lattin (1 ♂, 5 ♀); Lost Lake, on snow, 12 Jan. 1976, G. L. Peters (1 ♂); Potato Hill Road, near Lost Lake, on snow, 18 Jan. 1976 (1 ♀); 0.25 mi W of jct. Oregon Hwys 20 and 22, 4600 ft, on snow, 30 Dec. 1974, J. D. Lattin (1 ♂); 2.5 mi E of jct. Oregon Hwys. 20 and 22, 4500-5200 ft, near 0°C, 1 Feb. 1975, P. Johnson (2 ♀); Iron Mt., on snow, 31 Jan. 1981, L. Russell (5 ♂, 3 ♀); Pacific Coast Trail to N Santiam Pass, dead on snow, 20 Dec. 1980, L. Russell (2 ♂, 3 ♀); Sentinel Hills, Mt. Jefferson Wilderness, 4200-5500 ft, on snow, 22 Mar. 1981, L. Russell (1 ♂, 1 ♀); Marion Co., 1 mi W of Cheatcheek, about 3000 ft, 22 March 1975, R. J. Bury (1 ♂); Whitewater Creek, 14 mi NE Detroit, on snow, 3800 ft, 29 Mar. 1981, L. Russell (1 ♀); Polk Co., Laurel Mountain, 3000 ft, 21 Jan. 1978, L. Russell (2 ♂); Umatilla Co. (southeast), Bowman Meadows to Fly Creek, on snow, 16 Nov. 1962, J. Schuh (2 ♂); Union Co., from ice caves 10 mi S of Union, no date, R. Zack et al. (1 ♂, 17 ♀); Wallowa Co., Wallowa-Whitman National Forest, Eagle Cap Wilderness, 6000-7000 ft, weather clear, 24 Nov. 1972, A. Greene (2 ♂); same, but Lostine River, about 6000 ft, 27 Dec. 1974, no collector (1 ♀); same, but 3 Jan. 1975 (2 ♂); Wasco Co., 15 mi SE of Government Camp, Frog Lake Butte, 31 Dec. 1975, P. J. Johnson (4 ♂, 5 ♀). UTAH: Wasatch Co., Cascade Springs, Little Deer Creek, on snow, 29 Jan. 1966, E. C. Devenport (2 ♀). WASHINGTON: Chelan Co., near Wenatchee, No. 2 Cyn., 16 Dec. 1973, M. C. Hunter (1 ♀); Kittitas Co., near Lost Lake, S of Snoqualmie Pass, 3200 ft, on snow, about 1 per mile along logging road, 26 Nov. 1971,

J. S. Edwards (1♂, 2♀); Snoqualmie Pass, 1 Jan. 1976 (2♂); Spokane Co., Mt. Spokane State Park, 5000 ft, 9 Nov. 1975, A. Greene (5♂, 6♀); Yakima Co., 15 mi E of Chinook Pass, on snow about 2.5 ft deep, 17 Dec. 1977, P. J. Johnson (3♂, 6♀); near Yakima, 5000-6000 ft, on snow, April 1963 (1♂). YUKON TERRITORY: Evelyn Creek, near Whitehorse, on snow, 7 Jan. 1981, W. G. Johnston (2♂), same but 21 Feb. 1981 (2♀).

Chionea carolus BYERS

Chionea carolus Byers, 1979: 719-722.

Diagnosis.—A small, dark brown *Chionea* of the northern and central Sierra



FIGS. 163-170, *Chionea carolus*. 163, left antenna of male, lateral aspect. 164, gonapophyses, penis, vesica and its apodemes, right lateral aspect. 165, ninth abdominal tergum, left basistyle and left dististyle (tenth segment pushed inward to show gonapophyses), dorsal aspect. 166, left basistyle and dististyle, ventral aspect. 167, left hind femur, male, dorsolateral aspect. 168, right front femur and tibia, female, anterior aspect. 169, terminal abdominal segments, female, left lateral aspect. 170, ninth sternum and genital furca, female, ventral aspect. Scales: a—163-166, 170; b—167-169.

Nevada; antennae with four or five flagellomeres; male gonapophyses compressed, bowed outward near mid-length, convergent before acute apices, more than half length of basistyles; female cerci short, about 1.1 times length of hypovalves; ninth sternum formed of two subapically widened, apically bifurcate bands converging but not or barely in contact medially.

Description.—General appearance: Sclerites dark brown to brown, head blackish brown; membranous areas pale grayish brown; genital segment of male blackish brown; cerci of female amber brown. Femora in both sexes conspicuously thickened except slender near trochanteral attachments; hairs of legs relatively long. Length of male about 3-5 mm; female about 3.5-5 mm.

Head: Antennae (Fig. 163) comprising cylindrical scape, distally enlarged pedicel, long-conical fusion segment and three or four additional flagellomeres, the apical one very short. Setae of vertex stout but few and scattered. Eyes with about 70-90 ommatidia.

Thorax: Halteres pale grayish brown, conspicuously paler than dark brown thoracic dorsum. Femora slender and light brown to yellowish brown near attachments to trochanters, thickened and darker brown in both sexes through most of their lengths, especially noticeable in hind legs of male (Fig. 167) and fore legs of female (Fig. 168); seven or eight longitudinal rows of setae on femora, as well as a few scattered setae not in rows. Setae of tibiae nearly three times as long as tibial diameter, giving legs an unusually hairy appearance. Tarsi only about as dark as tibiae and femora.

Abdomen of male: Terga 1-8 with sparse, thick hairs along posterior margins, otherwise generally bare. Ninth tergum short, its posterodorsal emargination deep, U-shaped, extending nearly to base of tergum; no distinct lobes beside emargination but four to six long setae along margin at each side. Gonapophyses (Figs. 164, 165) proportionately large, more than half to nearly two-thirds length of basistyles, compressed, divergent near base but convergent just before slender, upturned, outwardly curved apices; penis curved downward at base, without other prominent curves, apex unmodified (Fig. 165); median, membranous pouch below gonapophyses with acute posteromedian margin. Basistyles only moderately thickened; posteromesal lobe darkly sclerotized, smooth (not pilose), with acute upper point and rounded lower one. Dististyles a little narrowed and most strongly curved near mid-length, with subacute but inconspicuous mesal tooth at base; ventral tooth not present. Ninth sternum with dense brush of dark yellowish brown setae near posterior median edge. Tenth (anal) segment membranous, small, protruding only to about mid-length of gonapophyses, of nearly uniform width throughout.

Abdomen of female: Terga 1-8 only sparsely hairy except for thick hairs along posterior margins; sterna more hairy and with scattered darkly pigmented spots. Eighth tergum darkly sclerotized throughout, short, slender, with slight dorsolateral thickening at each side (Fig. 169); lateral tips attenuate. Hypovalves of eighth sternum pale with darkened borders in apical two-thirds, brown basally; dorsal margin curved slightly ventrad toward acute apex, ventral margin smoothly upcurved, with a thin, translucent blade-like edge below marginal dark band. Genital furca (Fig. 170) lyre-shaped, narrowly joined to ninth sternum; latter in form of two convergent, strap-like extensions of lowermost corners of ninth tergum, each abruptly expanded before its shallowly bifurcate tip. Cerci short, approximately 1.1-1.2 times length of hypovalves measured from notch to tip, both dorsal and ventral margins evenly upcurved in lateral aspect; color dark amber brown.

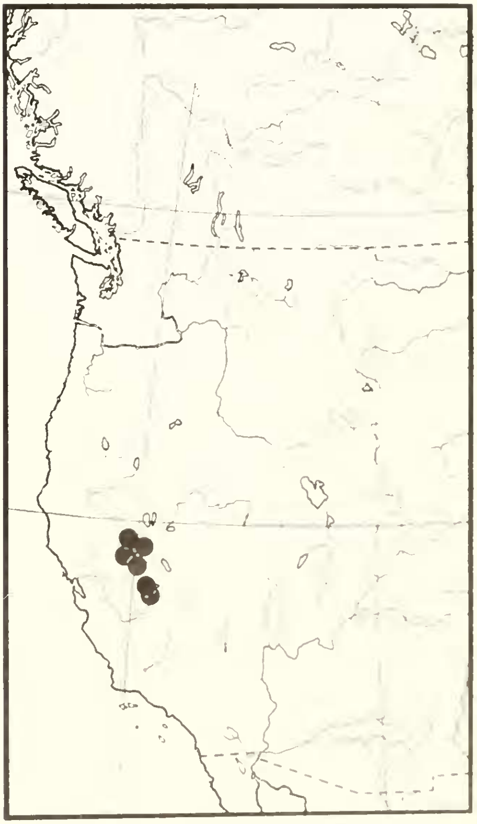
Types.—Holotype, male, 1 mi S of

Hobart Mills, on snow, 5800 ft (1770 m), Nevada Co., California, 20 Dec. 1971, N. D. Penny. Allotype and 1 ♂, 1 ♀ paratypes, same data as holotype. Additional paratypes: California, Placer Co., 3 mi N of Tahoe Vista, on snow, 7000 ft (2154 m), 20 Dec. 1971, N. D. Penny. Entire type series preserved in alcohol, in Snow Entomological Museum, Univ. of Kansas.

Variation.—Overall length of males varies from 2.6 and 2.9 mm in two extremely contracted specimens (i.e., with abdomens strongly "telescoped") to 4.9 mm in a robust individual. Most males, however, are in the range of 3-4.5 mm. Females seen measure 3.1-5.1 mm, with nearly a normal distribution of lengths. As noted in the description, the terminal flagellomere is short. Two individuals (1 ♂, 1 ♀) from Mariposa Co., California, have four unusually short flagellomeres beyond the fusion segment. Another male from the same locality has four flagellomeres (including fusion segment) on one side, five on the other. Although *carolus* is generally a hairy-looking *Chionea,* this is due largely to the setae of the legs; and individuals with shorter, less dense hairs than usual are not rare. Considerably less variation in robustness is found in males of *C. carolus* than in most species; that is, the smaller males are not characterized by slender femora and relatively slender basistyles. There exists some variation in the proportionate length of the ninth tergum, which is shorter than in most species. The degree of development and sclerotization of the mesal tooth of the dististyle differs considerably among males; and size variation in the gonapophyses has been noted in the description.

Relationships.—Although in general appearance *C. carolus* does not very closely resemble other members of the *alexandriana* group, I have placed it among them mainly on the basis of the male gonapophyses. Antennal structure supports this placement; so also does the short (narrowly transverse) eighth abdominal tergum of the female. All characters considered, *carolus* is probably most like *C. lyrata,* geographically its nearest neighbor, with which it shares part of its range. It may be readily differentiated from *lyrata* (and from other species of the *alexandriana* group in the Sierra Nevada) by its small size, overall hairiness and dark color, by the expanded femora with slender bases, by the shape of the male ninth tergum (deep emargination and lack of projections) and gonapophyses, and by the absence of the ventral tooth of the dististyle.

Geographic Distribution.—A species largely of middle elevations in the northern and central Sierra Nevada, *C. carolus* has to date been collected in Alpine, Mariposa, Nevada, Placer and Tuolumne coun-



Map 5. Range of *Chionea carolus.* Each spot represents one or more collections within a county.

ties in California and Washoe Co. in Nevada (Map 5). This is roughly from just north of Lake Tahoe to Yosemite National Park. In his detailed study of winter insects in Yosemite National Park, David Durbin found fairly consistent altitudinal separation of *carolus* from the higher montane *C. durbini* and other, less common members of the *alexandriana* group. Elevations of collection sites of *C. carolus* range from 5800-8600 ft (1770-2646 m).

Seasonal Distribution.—Most specimens were found in the period 8-25 December, yet one male was collected on 4 November and another on 2 February. Probably there is a single, prolonged emergence of the adults in late autumn and early winter.

Habitats.—The habitats of *carolus* are chiefly in the lower lodgepole pine zone or upper ponderosa pine-sugar pine zone of the Sierra Nevada. Durbin (1975: 8) described the habitat at Crane Flat, Yosemite National Park, as follows: "The dominant trees are *Abies magnifica* (red fir), *Pinus lambertiana* (sugar pine), *A. concolor* (white fir) and *P. murrayana* (= *P. contorta,* lodgepole pine); other prominent parts of the biota include *Libocedrus decurrens* (incense cedar), *Arctostaphylos* sp. (manzanita), *Ceanothus* sp. (mountain lilac), *Prunus* sp. and *Phyllodoce breweri* (mountain heather)." (Common names in parentheses added by me.)

Collection Records. — CALIFORNIA: Alpine Co., Carson Pass, 8600 ft (2646 m), on fresh snow 3-4 ft deep, overcast, light snowfall, 12:30-1:30 P.M., 14 Dec. 1974, D. Durbin (1♂, 1♀); Mariposa Co., Crane Flat Meadows, Yosemite National Park, 6200 ft (near 1900 m), from log in snow, 25 Dec. 1972 (1♂); same, but on snow, 2 Feb. 1973 (1♂); same, but 8 Dec. 1973 (2♂, 3♀); same, but during snowfall, 21 Dec. 1973 (1♀); same, but on 8-10 in of powdery snow, 23 Dec. 1973 (3♂, 7♀); all collected by David Durbin; Nevada Co., 1 mi S of Hobart Mills, on snow, 5800 ft (1770 m), 20 Dec. 1971, N. D. Penny (2♂, 2♀, including types); Placer Co., 3 mi N of Tahoe Vista, on snow, 7000 ft (2154 m), 20 Dec. 1971, N. D. Penny (2♂, 1♀, paratypes); Tuolumne Co., Crane Flat Meadows (area is partly in Mariposa Co.), Yosemite National Park, 6190 ft, 4 Nov. 1972, D. Durbin (1♂). NEVADA: Washoe Co., 3 mi E of Tahoe Vista, on snow, 20 Dec. 1971, N. D. Penny (1♂, 2♀).

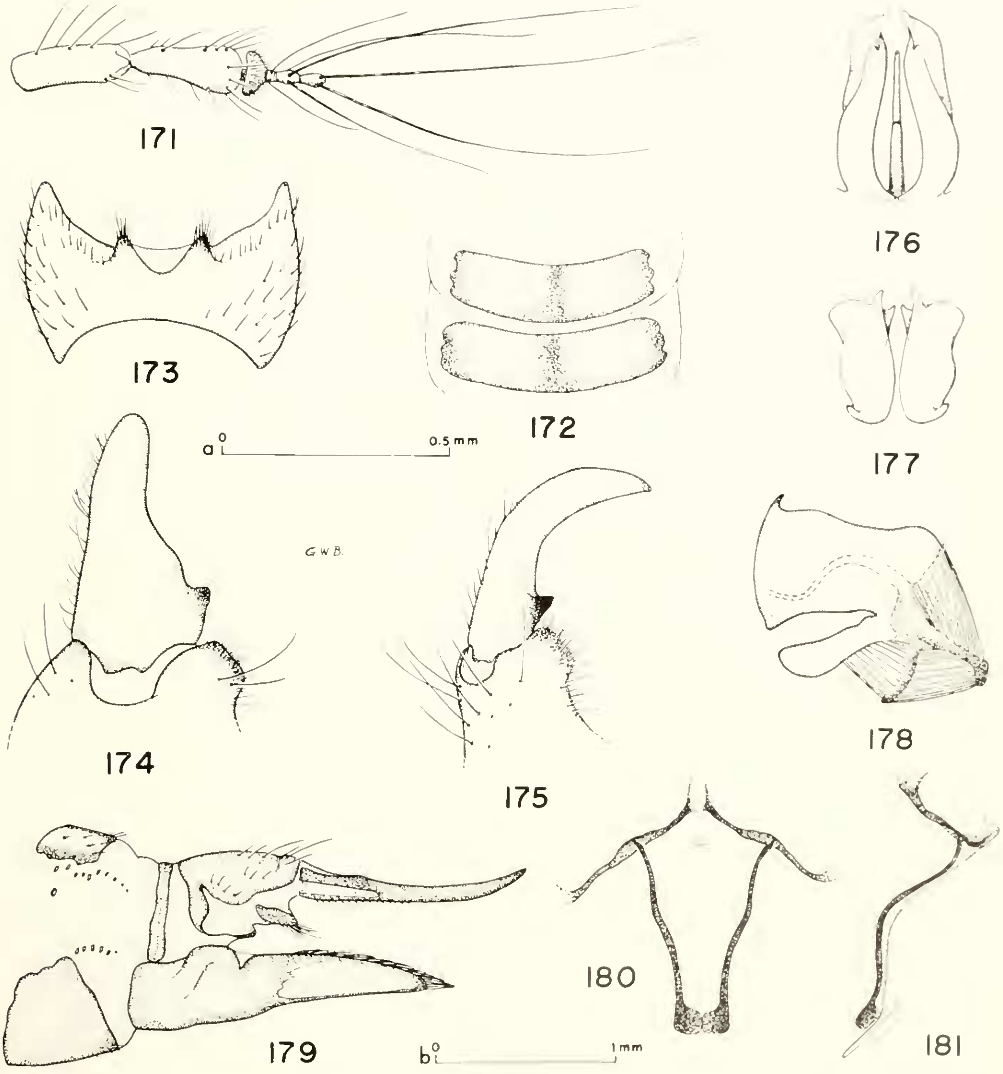
Chionea durbini, NEW SPECIES

Diagnosis.—A brownish species of the central, high Sierra Nevada of California, with two or three flagellomeres; legs long and slender, tarsi contrastingly darker; male gonapophyses compressed but curved to present a widened dorsal aspect, truncate at apex and bearing a small posterodorsal tooth; cerci slender, extending well beyond hypovalves, upturned slightly in apical half.

Description (based on 17♂, 17♀, preserved in alcohol).—General appearance: Overall color of sclerites dark yellowish brown to brown, membranous surfaces dull pale brown; genital segment of male dark brown in most specimens; ovipositor of female amber brown; legs conspicuously long, tarsi much darker than tibiae. Length of male normally contracted, about 4.7-7.7 mm; length of hind leg 8.3-13.2 mm; female, 5.9-9.6 mm, hind leg 7.8-10.2 mm.

Head: Antennae (Fig. 171) comprising subcylindrical scape about three times as long as its diameter, pedicel not quite as long as scape, broadly conical or turbinate fusion segment, and usually two additional flagellomeres (if three, most proximal one very short as in Fig. 171). Setae on vertex and occiput long, slender, brown. Compound eyes with 110-120 ommatidia each, more in males than in females.

Thorax: Halteres pale brown, contrasting noticeably with thoracic dorsum in most individuals. Hairs of mesonotum, pronotum and coxae numerous, long, slender, brown (not dark), longer on males than on females. Legs yellowish brown; hind femora of males only moderately incrassate, especially a little before midlength, those of females not noticeably enlarged. Femoral setae in seven longitudinal rows in females; setae much longer and with attenuate tips in males, in four rows on dorsal side of femur but very numerous and not in distinct rows on lower side. Basitarsi yellowish brown proximally, darkening to brown in apical half; other tarsomeres dark, blackish brown, in conspicuous contrast to leg color.



FIGS. 171-181, *Chionea durbini*. 171, right antenna of large male, lateral aspect. 172, two abdominal terga (anterior at top), to show color pattern. 173, ninth abdominal tergum, male, dorsal aspect. 174, left dististyle and apex of basistyle, robust male (holotype), posterior (ventral) aspect. 175, left dististyle of more slender male, posteromesal aspect. 176, gonapophyses and penis, dorsal aspect. 177, gonapophyses, posterior aspect. 178, same as 176, right lateral aspect; structure below gonapophysis is dorsally concave portion of floor of genital chamber. 179, terminal abdominal segments, female allotype, left lateral aspect. 180, ninth sternum and genital furca, allotype, posteroventral aspect. 181, same, left lateral aspect. Scales: a—171, 174-178, 180-181; b—172-173, 179.

Abdomen of male: Terga 1-8 brown along mid-line and posterior and lateral margins, otherwise lighter brown with scattered small brown spots (Fig. 172); setae longest along posterior margins, others arising from some of scattered spots; corresponding sterna more uniformly brown. Ninth tergum (Fig. 173) with broadly U-shaped posteromedian emargination; at each side of emargination a lobe about as long as its basal width, bearing approximately ten setae. Gonapophyses (Figs. 176-178) actually compressed blades but having undulating surface sloping downward and inward from upper, outer margin, such that they appear both in dorsal and posterior aspect to have considerable thickness; on upper margin of each, near posterior end, a small point or tooth directed upward. Penis sinuate, with unmodified apex (Fig. 178, dashed line). Basistyles with broad, pilose posteromesal lobe; dististyles (Figs. 174, 175) with subacute mesal tooth at base, ventral tooth rarely present (absent in holotype). Tenth segment lightly sclerotized laterally, narrowed near mid-length to about half basal width.

Abdomen of female: Terga 1-7 with median brown stripe and brown lateral margins, otherwise pale brown with scattered brown spots; sparse setae arising from spots. Eighth tergum (Fig. 179) short (i.e., slender) throughout, with thin, darkened, sclerotized line near mid-length, from side to side. Cerci long, slender, evenly upcurved in apical half to acute tip, extending well beyond ends of hypovalves. Hypovalves nearly straight along lower edge, dorsal edge gradually curved downward toward narrowly rounded apex; blades mostly translucent, with amber-brown borders; dark yellowish hairs along outer half to two-thirds of dorsal margin. Genital furca lyre-shaped, its slender arms bowed both outward (Fig. 180) and dorsad (Fig. 181). Ninth sternum formed of convergent strap-like prolongations of lowermost corners of ninth tergum, each widened near attachment of furca and expanded slightly and abruptly just before lightly sclerotized median portion.

Types.—Holotype, male, near Carnegie Institute Experimental Station, Inyo National Forest, Mono Co., California, on 2-6 in of snow, 9800-10,300 ft, 14 October 1973, collected by David Durbin. This locality is in the high Sierra Nevada west of Lee Vining, at approximately 37°58′N, 119° 17′W. Allotype, female, and 2 ♂, 7 ♀ paratypes, same data as holotype. Paratopotypes: 13 ♂, 8 ♀, 28 October 1973, at 9800 ft (3015 m). One ♂ paratype, Yosemite National Park, Tuolumne Co., California, on snow in Dana Meadows, 9900 ft, 22 October 1972, David Durbin (locality is SW of Lee Vining, about 2 mi W of the Sierra crest, which is the county line). One ♀ paratype, California, Mariposa Co., Yosemite National Park, Crane Flat Campground, 6200 ft (1908 m), on snow, 9 December 1973, David Durbin. Holotype, allotype, and most paratypes in the California Academy of Sciences, San Francisco; 3 ♂, 2 ♀ paratypes in the Snow Entomological Museum, Univ. of Kansas, Lawrence. One additional female, badly damaged, is recognized as belonging to this species but is not made a paratype; it is from 10,350 ft (3185 m) on Mt. Dana, Tuolumne Co., California, 29 Oct. 1972, collected by David Durbin.

Relationships.—Chionea durbini generally resembles *C. alexandriana*, its size, color and short antennae contributing to the similarity. On the basis of the gonapophyses and dististyles of the male and the eighth abdominal tergum and ninth sternum of the female, however, I judge this species to be most closely related to *C. carolus*, geographically its nearest neighbor. It may be differentiated from the smaller *C. carolus* by antennal structure, shape of femora, and details of male and female genital segments. Specifically, the usual number of flagellomeres in *durbini* is one fewer than in *carolus*, and the fusion segment is much shorter; the femora are much less incrassate in relation to their length; the gonapophyses of the male have an utterly different shape (cf. Figs. 176 and 164), and the cerci of the female of *durbini* are relatively much longer and more slender than in *carolus*.

This species is named for its collector, Mr. David Durbin, who has contributed greatly to our knowledge of *Chionea* and other winter insects of the Sierra Nevada through his collections and field observations.

Geographical Distribution.—This species is known only from the central Sierra Nevada of California, from about 1900-3200 m, in Mono, Tuolumne and Mariposa counties, which are contiguous (Map 6). Its range broadly overlaps that of *C. carolus*, although *durbini* generally occurs at higher elevations. It overlaps to a lesser extent the ranges of *excavata* and *lyrata* of the more northern Sierras and of the widespread *alexandriana*. Thus, *C. durbini* is the southernmost of the montane species of western North America.

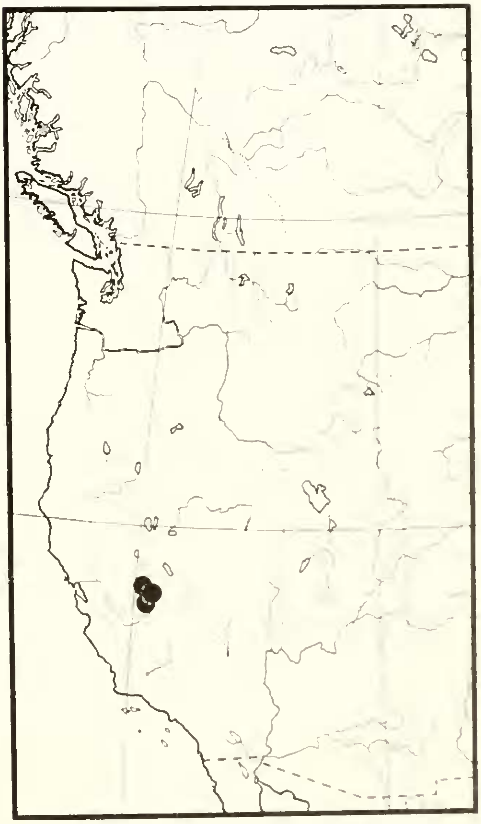
Seasonal Distribution.—Specimens from high elevations (above 3000 m) were collected from mid to late October; those collected in December are from the lower elevations recorded. It seems probable that the weather at the type locality and others in the high Sierras is too severe in December for *Chionea* to be active.

Habitats.—This is a species of high elevations in the Sierra Nevada, where the subalpine forest of lodgepole pine (*Pinus contorta*) and white-bark pine (*P. albicaulis*) is patchy, giving way here and there to small willows (*Salix* spp.) and Sierra junipers (*Juniperus occidentalis*) just below tree-line. At the Carson Pass locality, mountain hemlock (*Tsuga mertensiana*) and red fir (*Abies magnifica*) were additional forest trees. While the trees are, of course, not the habitat of *Chionea*, they characterize the general habitat.

Chionea excavata, NEW SPECIES

Diagnosis.—A western montane species of brown to grayish brown color, with antennae of four (rarely three) flagellomeres; male gonapophyses hooked at tip, dististyles shallowly concave on outer (upper) curvature; female cerci evenly curved, not much longer than hypovalves; ninth sternum mostly lightly sclerotized, with narrowly triangular darker median structure.

Description (based on 3 ♂, 7 ♀, pinned, and 2 ♂, 1 ♀, originally pinned but removed to microscope slides).—General appearance: Head dark brown, thorax brown to grayish brown; abdominal sclerites brown, except ninth segment of male dark



Map 6. Range of *Chionea durbini*. Each spot represents one or more collections within a county.

brown, cerci of female yellowish; pleural membranes light brown. Length of male about 4-6 mm, female about 6-7 mm, exclusive of antennae.

Head: Antennae (Fig. 182) comprising scape, pedicel and four flagellomeres (three in one specimen); fusion segment short-conical, its apical portion constricted at base in some specimens, resembling additional short segment. Eyes composed of about 80-100 ommatidia each.

Thorax: Halteres pale, contrasting with color of thoracic dorsum. Legs dark yellowish brown; seven (four dorsal, three ventral) longitudinal rows of setae on femora, sometimes an indication of fourth ventral row in male; tarsi brown.

Abdomen of male: Posterodorsal edge of ninth tergum (Fig. 183) with broadly V-shaped median emargination; at each side of emargination a low, blunt lobe bearing about six setae. Gonapophyses (Figs. 187, 188) broad at base, abruptly narrowed in distal half; apical portion hook-like, slender, curved upward, with blunt ventral heel-like process and acute tip; space between gonapophyses narrowly U-shaped; apex of penis unmodified. Basistyles thick, each with a bluntly rounded, pilose, posteromesal lobe (Fig. 184). Dististyles (Figs. 184-186) yellowish brown to reddish brown, thick at base, with blunt mesal tooth, somewhat flattened and shallowly excavated dorsally in apical half; excavated area largely pilose, also bearing scattered hairs as on remainder of outer (dorsal) surface of dististyle; ventral tooth small and blackened (holotype) to rudimentary. Tenth segment broad at base, narrowed near mid-length, darkly pigmented and pubescent laterally.

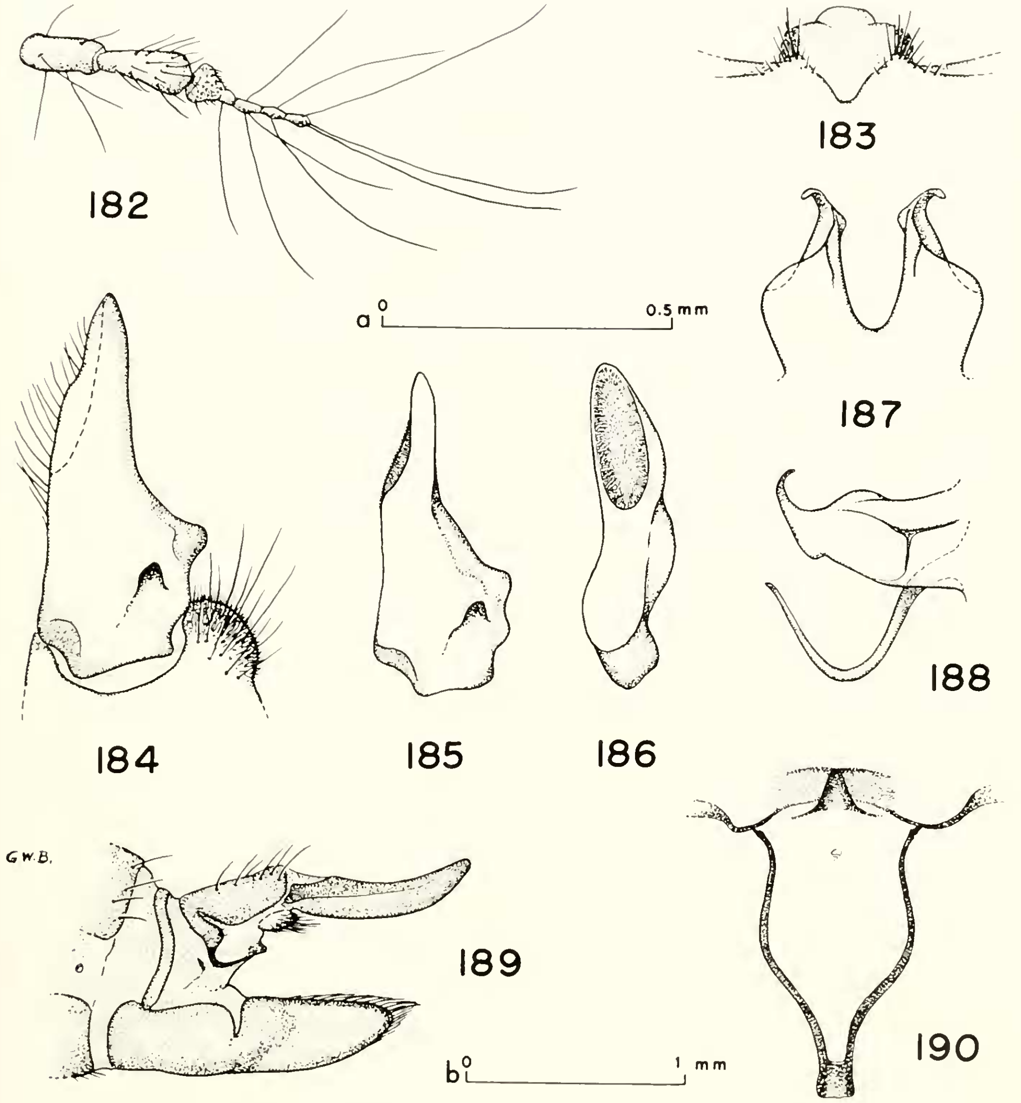
Abdomen of female: Eighth tergum short (i.e., slender) throughout. Hypovalves of eighth sternum deep, bluntly rounded at tip (Fig. 189), with lower margin more curved than dorsal margin. Arms of genital furca slender throughout; basal portion small, subrectangular, not much longer than wide. Ninth sternum with strongly sclerotized, narrowly subtriangular, projecting mid-ventral portion and a subquadrate, more lightly sclerotized and diffusely pigmented area above and to each side (Fig. 190). Cerci of medium length for genus, about 4.5-5 times as long as greatest width, evenly curved on both dorsal and ventral margins, about 1.2 times as long as hypovalves.

Types.—Holotype, male, 8 mi SW of Reno, Washoe Co., Nevada, elevation 7200-8200 ft, 19 January 1923, H. S. Barber collector. Allotype, female, same data as holotype. Paratypes: 1 ♂, 1 ♀, same data as holotype; 2 ♂, 4 ♀, northeast of Hunter Lake, Mount Rose, Washoe Co., Nevada, 7200-8200 ft, 19 January 1923; 2 ♀, near Caribou, Plumas Co., California, 27 December 1922; 1 ♂, near Caribou, Plumas Co., California, 24 January 1922 (1923?); all collected by H. S. Barber; 1 ♀, Washoe Co., Nevada, 3 mi E of Crystal Bay, 7300 ft, 20 Dec. 1971, N. D. Penny. Holotype, allotype, three male and six female paratypes in United States National Museum, Washington, D.C.; one male and one female paratypes (on slides) in Univ. of Michigan Museum of Zoology, Ann Arbor; one female paratype in Snow Entomological Museum, Univ. of Kansas, Lawrence.

Several female specimens from farther south in the Sierra Nevada apparently belong to this species. Since there are no associated males, however, these have not been made paratypes. All are in the collection of the California Academy of Sciences, San Francisco. The collection records are: CALIFORNIA: Alpine Co., Carson Pass, off California Hwy. 88, on snow, 8600 ft, 8:15 P.M., clear night, near 32°F, 14 Jan. 1975, D. Durbin (1 ♀); same place, but specimen found dead on snow, 1 P.M., clear day, 55°F, 15 Jan. 1975, D. Durbin (1 ♀); Mono Co., Inyo National Forest, Tioga Pass, Dana Meadows, 9900 ft, 26 Oct. 1968, R. P. Papp (2 ♀);

Inyo National Forest, Carnegie Inst. Exper. Sta., 28 Oct. 1973, D. Durbin (1 ♀); Tuolumne Co., Yosemite National Park, Mt. Dana, 11,000 ft, 29 Oct. 1972, D. Durbin (1 ♀); same general area, Dana Meadows, 10,000 ft, 15 April 1973, D. Durbin (1 ♀); same, but 16 April 1973 (1 ♀); same area, but Gaylor Peak, 11,000 ft, collected on snow, "6 VI 1973," D. Durbin (1 ♀) (Mr. Durbin states that the June date is correct but that the specimen may not have been alive when found).

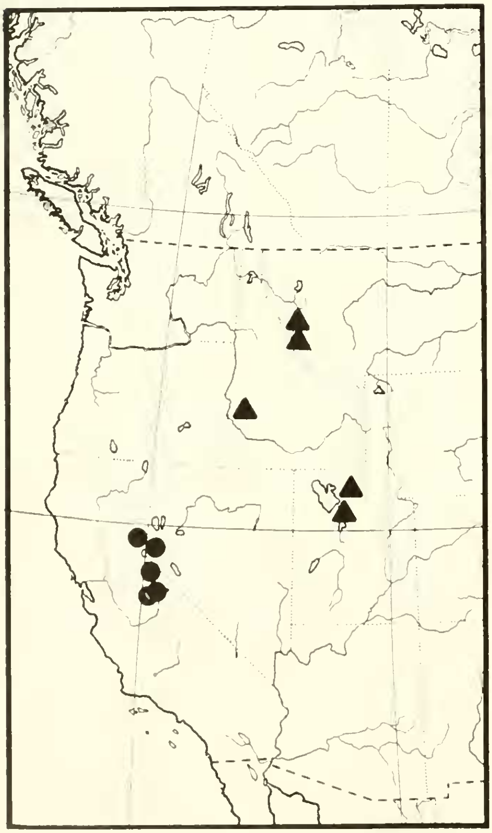
Variation.—Femoral setae in two of the males are very attenuate at the tip, many



Figs. 182-190, *Chionea excavata*. 182, right antenna of male, lateral aspect. 183, posteromedian portion of ninth abdominal tergum and tenth segment, male holotype, dorsal aspect. 184, left dististyle, robust male (holotype), posterior (ventral) aspect; depression in outer, upper surface indicated by dashed line. 185, left dististyle of more slender male, posterolateral aspect (large hairs omitted). 186, same, dorsolateral aspect (ventral surface to right). 187, gonapophyses, dorsal aspect. 188, right gonapophysis and penis, right lateral aspect. 189, terminal abdominal segments, female paratype, left lateral aspect. 190, ninth sternum and genital furca, composite from two females, ventral aspect. Scales: a—182-188, 190; b—189.

tips slightly curled. The cerci of the female vary from 1.1-1.2 times as long as the hypovalves (measured from notch to tip). Variation in color and size have already been mentioned. The holotype is a larger male than the others and is somewhat more darkly colored but was selected because both antennae were intact. It has a dried nematode capsule around its neck.

Relationships.—Chionea excavata belongs to the *alexandriana* group and within this group seems, on the basis of the male genital structures, particularly the gonapophyses, most nearly akin to *alexandriana* and *nigra*. From both these species it differs in general coloration and number of flagellomeres. Males of *excavata* can be distinguished from those of all other species by the shallowly concave tips of the dististyles; the specific name (Latin *excavata* = hollowed out) refers to this unique characteristic. There is a close resemblance between females of *excavata* and those of *lyrata* n. sp. in the structure of the ninth sternum; however, *excavata* has relatively shorter cerci, a smaller number of flagellomeres, and a less distinct color pattern on the abdominal terga. In lateral aspect, the ventral margins of the hypovalves in *excavata* are more curved than the dorsal margins, while in *lyrata* both margins curve about equally toward the bluntly rounded apex.



Map 7. Ranges of *Chionea excavata* (circles) and *C. jellisoni* (triangles). Each symbol represents one or more collections within a county.

Geographic Distribution.—This seems to be a species of the upper slopes (2215-3385 m) of the northern and central Sierra Nevada of California and westernmost Nevada (Map 7). So few specimens are known that the actual range is still unclear. This is the "species 1" recorded by Alexander (1967: 121), who through a misunderstanding reported the holotype from California (because I had sent him only the California records for the species).

Seasonal Distribution.—The very wide span of dates on which adults have been found, from late October to at least mid-April, suggests there may be two generations per year. The June collection record is unusual, yet not particularly to be doubted; apparently, suitable environmental conditions still prevailed at the time the specimen was collected.

Habitats.—Elevations in the Sierra Nevada at which *C. excavata* has been collected are mainly subalpine, characterized by mixed coniferous forests of lodgepole pine (*Pinus contorta*), white-bark pine (*P. albicaulis*), red fir (*Abies magnifica*), mountain hemlock (*Tsuga mertensiana*), and western or Sierra juniper (*Juniperus occidentalis*). The higher recorded sites are near local tree-line, where the white-bark pine and small junipers and willows are characteristic vegetation.

Chionea jellisoni, new species

Diagnosis.—A western montane species with antennae having three flagellomeres; male gonapophyses broad at base with slender tips turned upward and outward; female cerci curved evenly upward in apical half, very short (not quite as long as hypovalves) but wide in dorsal aspect, especially in basal half.

Description (based on 31 ♂, 50 ♀ preserved in alcohol, 7 ♂, 6 ♀ pinned).—General appearance: Head reddish brown to dark brown, antennae and mouthparts slightly paler; thorax dark yellowish brown to brown, a little paler dorsally between halteres; abdominal sclerites yellowish brown to light brown except ninth segment of male reddish brown to dark brown; pleural membranes pale, dull yellowish brown; cerci and apical half of hypovalves of female translucent yellowish. Length of male, exclusive of antennae, about 5.0-5.8 mm (holotype 5.8 mm); length of female about 6.5-7.4 mm (allotype 7.2 mm).

Head: Antennae (Fig. 191) comprising scape and pedicel of about equal length, and three flagellomeres; fusion segment broadly conical, slightly asymmetrical, wider than long, with apex somewhat prolonged, giving appearance of another short flagellomere; terminal hairs of flagellum a little longer than all antennal segments together. Setae on vertex pale yellowish brown to light brown. Compound eyes with about 140-150 ommatidia each.

Thorax: Color abruptly paler than that of head, evenly dark yellowish brown or brown, except for paler area on metathoracic dorsum. Halteres yellowish to brownish gray, slightly darker than abdominal pleura but not conspicuously paler than thoracic sclerites generally. Setae of mesonotum long, stout, not darkly sclerotized, in two longitudinal patches. Legs yellowish brown to light brown; tarsi only slightly darker than femora and tibiae. Femora with six or seven well defined rows of dark brown setae; tibial setae more slender than those of femora, slightly longer, also in readily discernible rows.

Abdomen of male: Terga and sterna evenly pigmented, without evident color pattern, except diffuse paler spots on terga of some individuals; tergal setae sparse, short, mostly along posterior margins of terga; sternal setae longer, more dense, especially at sides of sterna. Posterodorsal margin of ninth tergum (Fig. 192) with two prominent lobes separated by broadly V-shaped incision; approximately six setae of various lengths on or near apex of each lobe; setae laterad from lobes often longer than those on lobes. Gonapophyses (Figs. 193, 195, 196) broad in basal half, with slightly concave dorsal surface irregularly and shallowly emarginate at posterior edge; apical half becoming abruptly narrowed to elongate, slender, hook-like tip curving upward and outward; gonapophyses nearly in contact slightly beyond midlength; apex of penis unmodified. Basistyles thick, their posteromesal lobes bluntly rounded or with two low prominences, with scant pilosity. Dististyles (Fig. 194) slightly paler than basistyles, evenly curved on outer surface, ridged along most of inner curvature except near mid-length, somewhat expanded slightly beyond midlength. Mesal tooth of dististyle prominent, broadly subconical; ventral tooth also prominent, darkly sclerotized, usually with short, chisel-like apex (more nearly conical in holotype). Tenth segment only lightly sclerotized and pigmented laterally.

Abdomen of female: Terga and sterna uniformly pigmented; setae sparse, not much darker than sclerites, distributed about as in male. Eighth tergum a narrow, transverse strap, at widest (i.e., longest) only about one-third length of seventh tergum, without setae. Hypovalves deep, only slightly longer than basal portion of eighth sternum, with both upper and lower margins curving gently toward tips. Cerci slightly shorter than hypovalves (ratio of 0.94 to 1.0), depressed, appearing of about uniform width throughout in lateral aspect (Fig. 199) but actually conspicuously widened in basal half (Fig. 197b), tapering toward acutely rounded apices. Ninth tergum without posterolateral setae; tenth tergum short, wide, with only slight indication of transverse sulcus near posterior margin (Fig. 197b). Basal portion of genital furca longer than wide, weakly sclerotized medially; arms of furca strongly bowed outward near mid-length, thickened near bases (Fig. 200). Median portion of ninth sternum more densely sclerotized marginally than centrally, slightly concave ventrally, with bluntly rounded median tooth and irregular, lightly pigmented areas in adjacent membrane (Figs. 200, 201).

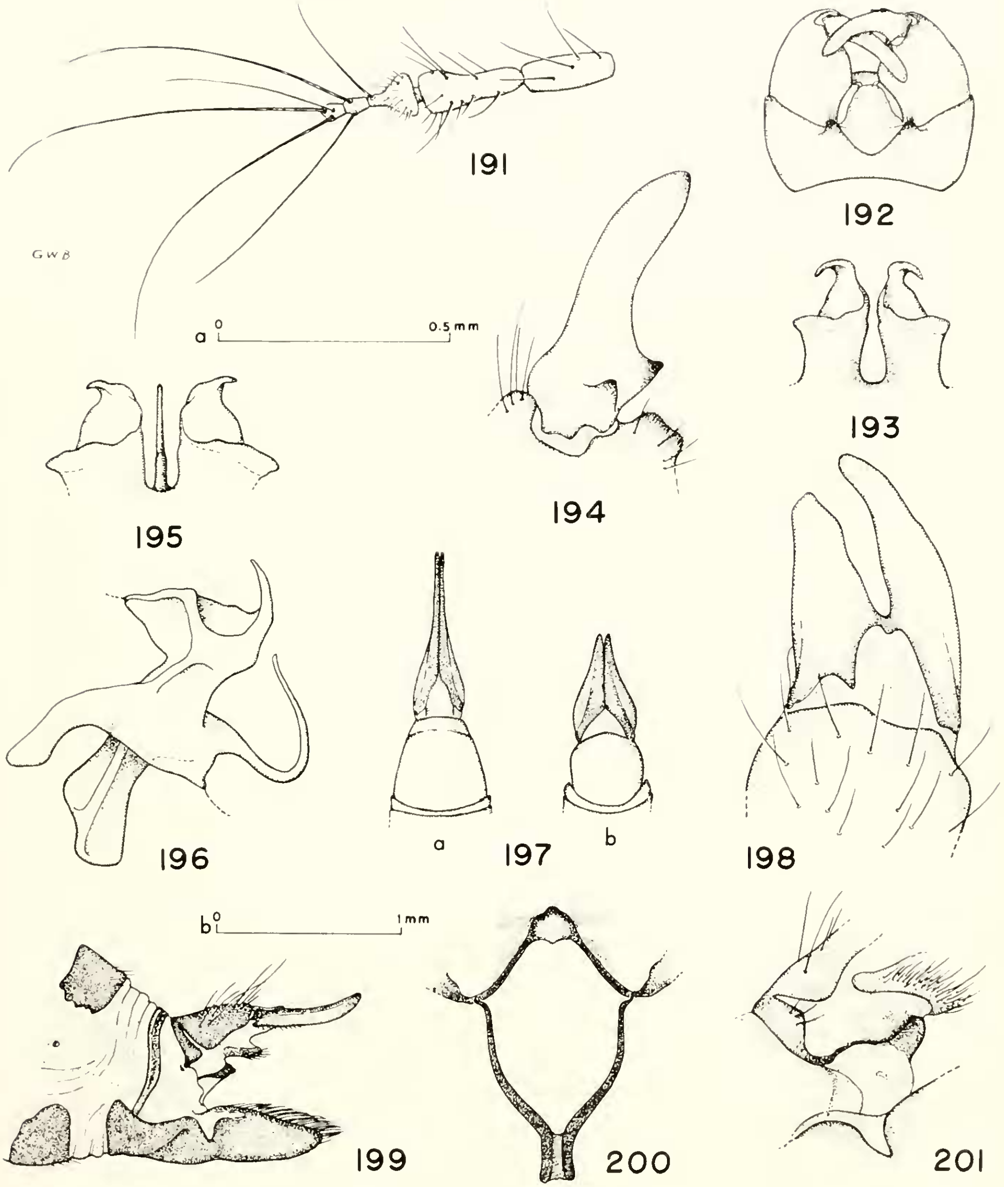
Types.—Holotype, male, Boulder Creek, Ravalli Co., Montana, on snow, 9 December 1956, collected by W. L. Jellison and R. Scott. Allotype, female, and 1 ♂, 4 ♀ paratypes, same data as for holotype. Additional paratypes: MONTANA: Ravalli Co., West Fork Boulder Creek, on snow, 29 Jan. 1966, W. L. Jellison (1 ♀); Lake Como Road, on snow, 27 Nov. 1965, W. L. Jellison (2 ♀); Tin Cup Canyon, 3 mi W of Darby, on snow, 1 Dec. 1970, W. L. Jellison and J. E. Keirans (2 ♂, 3 ♀, including a mating pair); Missoula Co., Elk Creek, Lubrecht Forest, 4000 ft, 22 Jan. 1972, R. A. Haick (14 ♂, 25 ♀, including one mating pair). IDAHO: Boise Co., 0.25-0.5 mi E of Idaho City, 21 Dec. 1974 (4 ♂); same, but on snow in pine forest, 7 Dec. 1974 (1 ♂); 11 mi N of Idaho City, on snow in pine forest, 7 Dec. 1974 (1 ♀); same locality, 30 Nov. 1974 (2 ♀); Idaho City, 14 Dec. 1974 (1 ♂); same locality, on snow, 16 Jan. 1976 (1 ♂, 2 ♀); T5N, R3E, Sect. 18, on snow at Bogus Basin, 27 Feb. 1977 (1 ♀); all collected by G. A. Shook. UTAH: Cache Co., Logan Canyon, Spring Hollow, near reservoir, on snow, 12 Nov. 1968, B. Geils (1 ♀); Salt Lake Co., Alta, on snow, 8585 ft, 12 Feb. 1975, K. J. Goeden (14 ♂, 13 ♀). Holotype, allotype and some paratypes in the Snow Entomological Museum, Univ. of Kansas; paratypes also in collections of W. L. Jellison (Hamilton, Montana), Univ. of Montana, and Utah State Univ. The type locality, Boulder Creek, is a tributary of the West Fork of the Bitterroot River, draining the north slope of Boulder Peak, in southwestern Ravalli Co.

Five females from Salt Lake Co., Utah, are identified as *C. jellisoni* but have not been made paratypes because of lack of associated males. These are: Neffs Canyon, 10 March 1966, R. W. Baumann (2 ♀); Albion Basin, Alta, 9 Feb. 1976, K. J. Goeden (3 ♀). Four of these females are much larger than others from the Wasatch Mountains and are darker, somewhat resembling females of *C. nigra*. At their type localities in Montana and Colorado, *jellisoni* and *nigra* are very different, but in Utah they seem to converge particularly with respect to color.

This species is named for Dr. William L. Jellison, renowned medical entomologist and collector of many of the type series. I am indebted to him not only for numerous specimens of *Chionea* and other winter insects but also for his good company on entomological walks in the forest in Montana and, many years ago, in Korea.

Variation.—One sees the usual variation in size in both sexes of *C. jellisoni* and in robustness in males. However, the degree of variation in number of antennal flagellomeres so common in other species is not found in this one. Virtually every specimen seen has two flagellomeres beyond the fusion segment; a short third one is rarely present.

Only once among the hundreds of specimens examined have I seen a developmental anomaly of the ovipositor. This is in a female of *jellisoni* from Boulder Creek, Ravalli Co., Montana (Fig. 198). The right cercus is short and thickened,



Figs. 191-201, *Chionea jellisoni.* 191, left antenna, male holotype, lateral aspect. 192, ninth and tenth abdominal segments, holotype, dorsal aspect (most setae omitted). 193, gonapophyses, holotype, dorsal aspect. 194, left dististyle, holotype, posterior (ventral) aspect. 195, gonapophyses and penis, male from Utah, dorsal aspect. 196, gonapophyses, penis, vesica and its apodemes, male from Utah, left lateral aspect. 197a, b, comparison of tenth tergum and cerci, dorsal aspect, of females of *C. alexandriana* (a) and *C. jellisoni* (b), both from Missoula Co., Montana. 198, deformed cerci, female from Ravalli Co., Montana, dorsal aspect. 199, terminal abdominal segments, female allotype, left lateral aspect. 200, ninth sternum and genital furca, composite of two females, ventral aspect. 201, details of ninth and tenth segments, female, ventrolateral aspect. Scales: a—191, 193-196, 198, 200-201; b—192, 197, 199.

the left one of nearly normal length but apically curved toward the right side. Both cerci are badly deformed, as shown.

See under Types, above, concerning variations in some females from Utah that converge on the form of *C. nigra.*

Relationships.—Within the *alexandriana* species group, *C. jellisoni* is most similar in nearly every character to *alexandriana,* a species whose range it broadly overlaps. It is rarely the case that females of a species of *Chionea* can be more readily differentiated than males, but this is true of *jellisoni* and *alexandriana.* The most conspicuous difference is the cerci, which are much longer than the hypovalves and extend well beyond them in *alexandriana,* but which are slightly shorter than or about equal to the hypovalves in *jellisoni* (cf. Figs. 160, 199). In dorsal aspect, the difference is even more striking (Fig. 197a, b). There is also a difference in shape of the tenth abdominal tergum, in dorsal aspect (Fig. 197), and the transverse sulcus near the posterior end of this tergum is faintly developed in *jellisoni* but clearly impressed and usually somewhat pigmented in *alexandriana.* The median plate of the ninth sternum of *alexandriana* ordinarily is uniformly densely sclerotized, with three distinct posterior teeth, while in *jellisoni* it is more densely sclerotized along the margins and has only broadly rounded, indistinct posterior teeth as well as a small anterior point directed toward the aperture of the bursa copulatrix (Fig. 200).

Recognition of males is less easy. In general, the posterior margins of the broad, basal portion of the gonapophyses are more uneven and project farther laterad than in *alexandriana* (cf. Figs. 193, 195 and 156). The upturned apical hook is thicker in *jellisoni* and lacks the ventral, heel-like process seen in *alexandriana* (Figs. 196, 157). The ventral tooth of the dististyle is usually more strongly developed in *jellisoni,* in equally robust males of the two species. Actually, overall dorsal aspect is fairly reliable in this differentiation. The abdominal terga of *jellisoni* are unicolorous or nearly so, and the hairs on the terga are short, sparse, and occur mainly along the posterior tergal margins. In contrast, in *alexandriana* the terga are darker anteriorly, laterally and along the dorsal mid-line, and the hairs are longer than in males of *jellisoni* of equal size and are more evenly scattered over the tergum.

Earlier I have mentioned the problem of the relationship of *jellisoni* to the similar *C. nigra* in Utah, where the two are in contact.

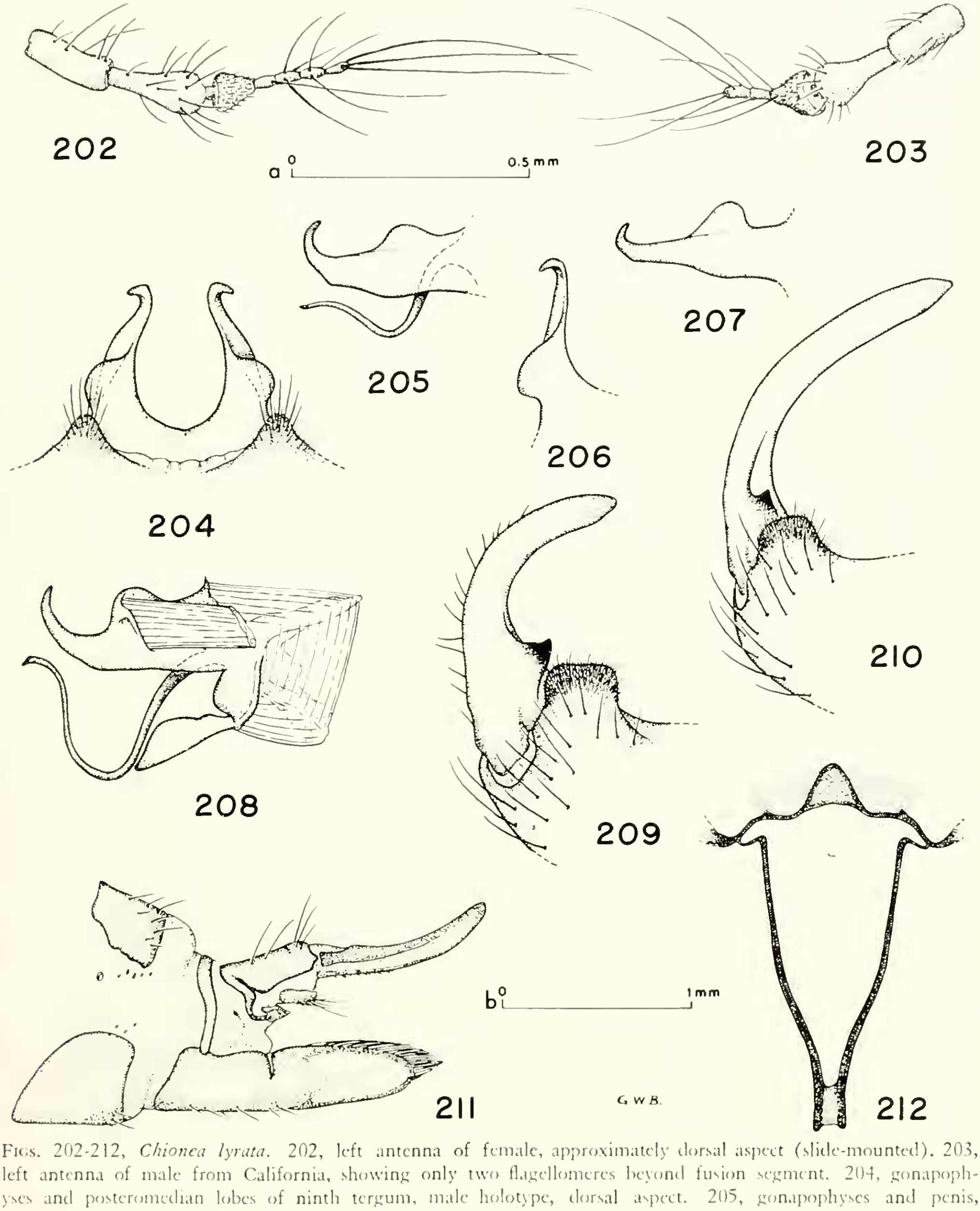
Geographic Distribution.—As now known, the range of *C. jellisoni* extends from west-central Montana, especially the Bitterroot Range, southwestward through the Salmon River Mountains to the vicinity of Boise, Idaho, and southward through the Wasatch Range into northern Utah (Map 7). At the type locality the elevation is near 5000 ft (1538 m; elevations along Boulder Creek below Boulder Falls are from 4600-5400 ft). At the Lubrecht Forest site it is near 4000 ft (1231 m). At the southern end of the range, *C. jellisoni* was taken at 8585 ft (2642 m).

Seasonal Distribution.—Collection dates are spread rather evenly from late November to late February, but 70% of the individual specimens were taken in approximately the last month of this span. This probably represents a single but prolonged period of adult emergence.

Habitats.—At middle elevations, including the type locality, the forest macrohabitat of *C. jellisoni* is characterized by western yellow pine (ponderosa pine, *Pinus ponderosa*) and Douglas fir (*Pseudotsuga taxifolia*). At the higher elevations lodgepole pine (*P. contorta*) is the dominant conifer. In Ravalli and Missoula counties, Montana, the habitats are characterized further by approximately 30-degree slopes strewn with granitic boulders among the pines and firs. It was my impression that these areas would be fairly dry near the surface in summer, while in winter they were covered with deep snow (2-3 ft and drifted deeper).

Chionea lyrata, new species

Diagnosis.—A western montane species, light brown to brown in color, with four or five antennal flagellomeres (rarely few-



Figs. 202-212, *Chionea lyrata*. 202, left antenna of female, approximately dorsal aspect (slide-mounted). 203, left antenna of male from California, showing only two flagellomeres beyond fusion segment. 204, gonapophyses and posteromedian lobes of ninth tergum, male holotype, dorsal aspect. 205, gonapophyses and penis, holotype, right lateral aspect. 206, variant form of right gonapophysis, dorsal aspect. 207, same, right lateral aspect. 208, right gonapophysis, penis, vesica and its apodemes and muscles, and portion of floor of genital chamber, right lateral aspect. 209, left dististyle and apex of basistyle, male from Placer Co., California, ventromesal aspect (somewhat foreshortened). 210, same, mesal aspect. 211, terminal abdominal segments, female paratopotype, left lateral aspect. 212, ninth sternum and genital furca, reconstructed from slide-mounted specimen, ventral aspect. Scales: a—202-210, 212; b—211.

er), fusion segment subconical; male gonapophyses curved widely apart at base, somewhat convergent before apex, hooked upward at tip; female cerci upturned in distal half, clearly longer than hypovalves.

Description (based on 1 ♂, 3 ♀, pinned but apparently originally preserved in alcohol, one male, one female, removed from pins to microscope slides, and one male, one female in alcohol).—General appearance: Head dark brown, thorax brown; abdominal sclerites yellowish brown to brown, terga darker brown along mid-line and at lateral edges, ninth segment of male dark reddish brown, cerci of female yellowish; pleural membranes tan. Length of male about 4-7 mm, female about 4-8 mm, exclusive of antennae.

Head: Antennae (Fig. 202) comprising scape, pedicel and four or five flagellomeres; fusion segment subconical, its apical portion in some individuals constricted at base, resembling additional short segment. Eyes with about 140-160 ommatidia each.

Thorax: Halteres very pale, contrasting with color of thoracic dorsum. Legs yellowish brown; seven (four dorsal, three ventral) longitudinal rows of setae on femora; tarsi brown beyond mid-length of basitarsus.

Abdomen of male: Posterodorsal edge of ninth tergum (Fig. 204) with broadly U-shaped median emargination; at each side of emargination a small, blunt lobe bearing six or seven large setae and a few smaller ones. A patch of long, pale setae near posteromedian margin of ninth sternum. Gonapophyses (Figs. 204-208) somewhat widened at base, with rounded, dorsolateral flange, narrowing in distal half; apical portion hook-like, slender, curved upward, acute at tip, without ventral process; space between gonapophyses widest near mid-length, narrowed posteriorly; apex of penis unmodified. Basistyles thick, posteromesal lobe of each pilose, with two rounded protuberances in some individuals. Dististyles (Figs. 209, 210) long, slender, yellowish brown, palest apically, thick at base with blackened mesal tooth, narrowing abruptly, then evenly curved, more or less circular in cross-section, and smoothly tapering to tip; ventral tooth small and blackened, or rudimentary and not darkened, or absent. Tenth segment wide at base, narrowed near mid-length, a little pigmented laterally.

Abdomen of female: Eighth sternum short (i.e., slender) throughout. Hypovalves of eighth sternum deep, obtusely rounded at tip (Fig. 211). Arms of genital furca slender throughout; basal portion small, not much longer than wide. Ninth sternum with well-sclerotized, projecting, subtriangular, mid-ventral portion and a rounded, less densely sclerotized area above and to each side (Fig. 212). Cerci elongate, about 5.5 times as long as greatest width, curved upward in apical half, noticeably longer than hypovalves (ratio about 1.3 to 1).

Types.—Holotype, male, near Seneca, Plumas Co., California, 28 December 1922, H. S. Barber collector. Allotype, female, same data as holotype. Paratypes: 2 ♀, same data as holotype except one without date on label; 1 ♂, same locality as holotype but dated 23 Jan. 1923; 1 ♀, Sunnyside, near Seneca, Plumas Co., California, 25 Dec. 1922, all collected by H. S. Barber; 1 ♂, 1 ♀, 3 mi N of Tahoe Vista, Placer Co., California, on snow, 7000 ft, 20 Dec. 1971, N. D. Penny.

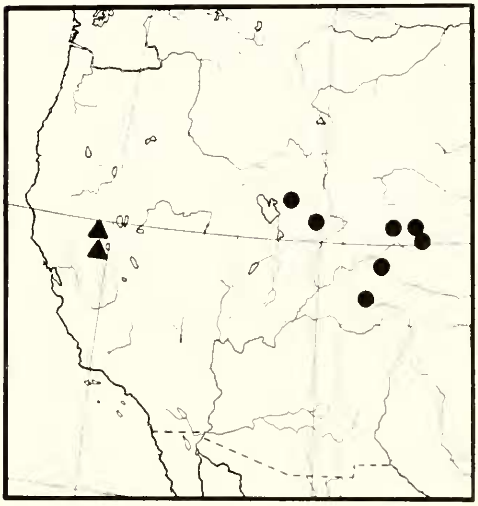
The type locality, Seneca, is on the North Fork of Feather River, 4.5 mi (7.2 km) south of the dam at the south end of Lake Almanor, in Plumas National Forest. Sunnyside is 2 mi southwest of Seneca. Holotype, allotype, and two female paratypes in the U.S. National Museum of Natural History, Washington, D.C.; male paratype and female paratopotype (on slides) in Univ. of Michigan Museum of Zoology, Ann Arbor; one male, one female paratypes in Snow Entomological Museum, Univ. of Kansas, Lawrence.

Variation.—About half the specimens have three flagellomeres beyond the fusion segment, the others four (with one exception), so that neither count can, on the basis of the small number of specimens available, be said to be typical. In the holotype the number is three, in the allotype three in one antenna and four in the other. The male from Placer Co. has only two flagellomeres beyond the fusion segment (Fig. 203). Some of the specimens do not show the dorsal abdominal color pattern as clearly as do the holotype and allotype; and certain of the females have the abdominal pleural membranes fading from tan to whitish on the eighth and ninth segments. The holotype is a large male, 7.2 mm in length, its abdomen not telescoped, possibly as a result of the specimen's having been originally preserved in alcohol. Such preservation might also account for the somewhat bleached appearance, especially of the halteres and membranes, of the type and other specimens. It also might have accentuated the dorsal color pattern. In the holotype, the blackened lobe at the base of the dististyle is truncate at its tip, with a sharp, somewhat chisel-like edge (cf. Figs. 209, 210).

Relationships.—Although it differs a little from the other species of the *alexandriana* group in the structure of the gonapophyses, *Chionea lyrata* clearly can be placed with them on the basis of a combination of characters. It most closely resembles *C. excavata* in this species group. Comparison of Figures 204-205 and 187-188 will show that in spite of the evident differences in the gonapophyses the general form is the same. The specific name *lyrata* (from Greek *lyra*) is suggested by the lyriform arrangement of the gonapophyses. With respect to antennal structure, both the number of flagellomeres and the shape of the fusion segment, *lyrata*, is most like *excavata*. In the shapes of the genital furca and ninth sternum of the female, also, these two species are very similar. Their males may be distinguished easily by reference to the dististyles and gonapophyses, but the females may be recognized only by such less definite characters as the greater length and uneven curvature of the cerci and the more evident abdominal color pattern in *lyrata* (see discussion under *excavata*). The number of flagellomeres provides an indication of the species but is not altogether reliable. I do not know what variation in this (or any other) character a larger sample might show.

Geographic Distribution.—Only two localities are recorded for this species, both in the northern Sierra Nevada of California and only 80 mi (128 km) apart (Map 8). The known range extends approximately from Lake Tahoe northwestward to Lake Almanor. At Seneca the elevation is 3600 ft, but immediately adjacent slopes are 4400 ft (1354 m) and higher. Barber did not record how near the village, on Feather River, the Chioneas were taken.

This is the "species 2" recorded by Alexander (1967: 121). The range given by Alexander reflects my early confusion of



MAP 8. Ranges of *Chionea lyrata* (triangles) and *C. nigra* (circles). Each symbol represents one or more collections within a county.

this species with certain individuals of *C. alexandriana.*

Seasonal Distribution.—This species has been found only during December and January, suggesting a single annual generation. Since the region in which *lyrata* was collected has been little explored for winter insects, it would be premature to exclude the possibility of a much longer period of adult emergence (as for other Sierran species) or even a second generation in March and April.

Habitats.—This seems to be a species of the Transition zone, or of middle elevations in the Sierra Nevada, where the dominant forest trees are ponderosa pine (western yellow pine, *Pinus ponderosa*), sugar pine (*P. lambertiana*) and white fir (*Abies concolor*). In the vicinity of Lake Tahoe, red fir (*A. magnifica*) and lodgepole pine (*P. contorta*) are also present. I have not seen the type locality but have several times traversed the more southern part of this range and found it generally dry and agreeably cool (for humans) in summer and deeply blanketed with snow in winter.

North of Tahoe Vista, *C. lyrata* was taken together with the smaller, darker *C. carolus.*

Chionea nigra, NEW SPECIES

Diagnosis.—A species of the central Rocky Mountains, black in overall color; antennae with two to four flagellomeres; male gonapophyses broad at base, slender and turned upward and laterad at tips; female cerci evenly curved, only slightly longer than hypovalves.

Description (based on 5 ♂, 7 ♀, pinned, 3 ♂, 4 ♀, in alcohol, and 2 ♂ 2 ♀, originally preserved in alcohol but removed to microscope slides).—General appearance: Macroscopically, overall color black. Microscopically, head black, thorax and abdomen dark brownish black, all with velvety texture; ninth segment of male black, cerci of female dark amber-brown. Length of male about 4.5-6 mm, pinned, to 8 mm on slide; female about 5-7 mm, pinned, to 8 mm on slide.

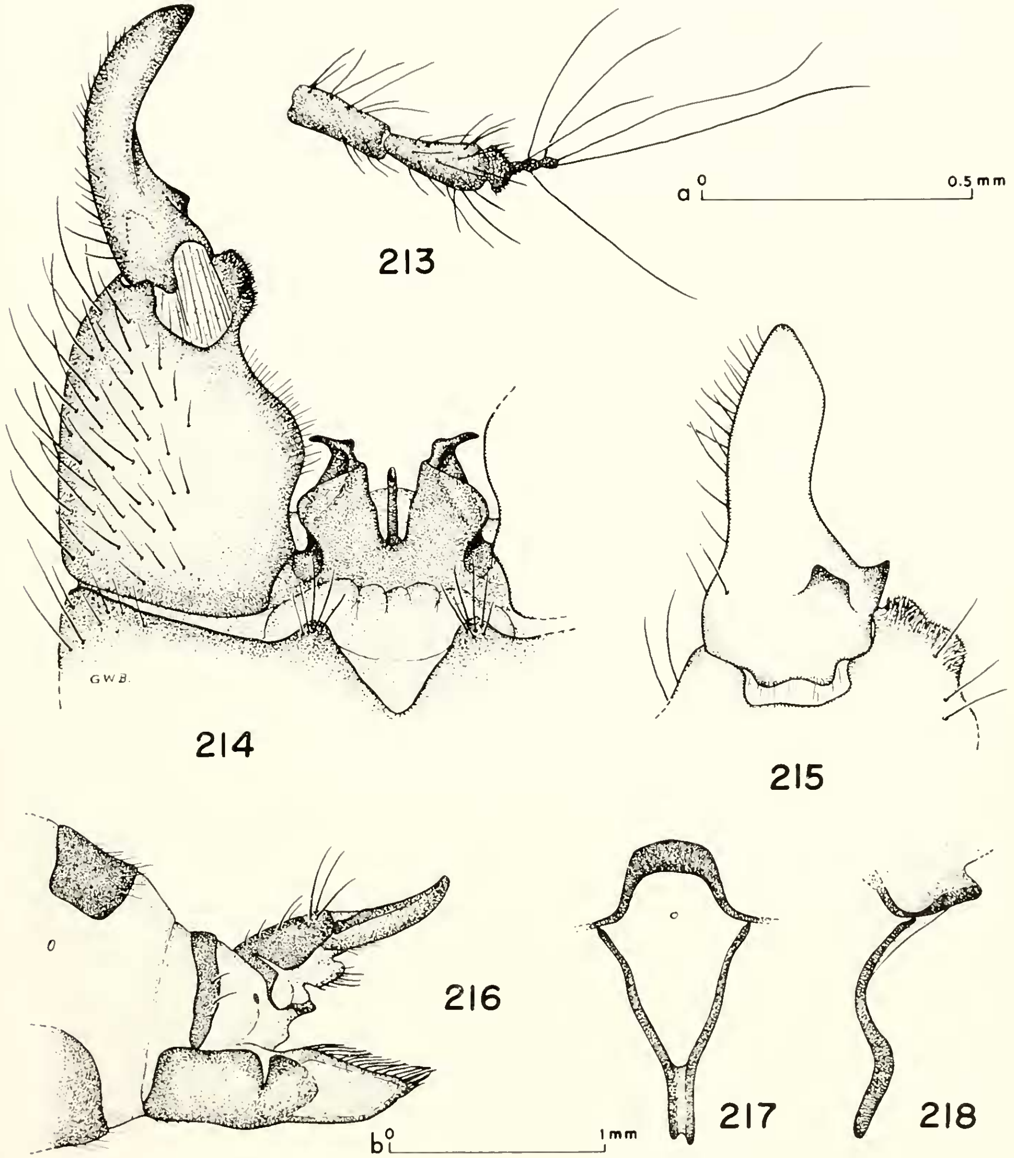
Head: Antennae (Fig. 213) consisting of scape, pedicel and usually three but rarely two or four flagellomeres; fusion segment short, broadly turbinate. Eyes with about 120-140 ommatidia each.

Thorax: Halteres dusky brown, not conspicuous by contrast with thoracic dorsum. Legs dark brownish black to blackish; seven or eight longitudinal rows of setae on femora, in female, to 11 (6 dorsal and 5 ventral), in larger males, the rows sometimes indistinct; tarsi black.

Abdomen of male: Posterodorsal edge of ninth tergum (Fig. 214) with broadly V-shaped median emargination; at each side of emargination a small, blunt lobe bearing about six setae. Gonapophyses (Fig. 214) broad at base, upper surface abruptly narrowed in distal one-third; apical portion hook-like, with a blunt ventral process, slender, curved upward and outward to acute tip; space between gonapophyses narrowly U-shaped; apex of penis unmodified. Basistyles thick, posteromesal lobe of each pilose, with two rounded protuberances (Fig. 215). Dististyles (Figs. 214, 215) dark reddish brown, thick, with blunt or sometimes truncate ventral tooth near base, narrowest and most strongly curved near mid-length, subacute at apex; mesal tooth sharply pointed, blackened, of variable size but present in all males examined. Tenth segment wide at base, narrowed a little beyond mid-length, lightly pigmented laterally.

Abdomen of female: Eighth tergum short (i.e., slender) throughout, less than one-third length of seventh tergum. Hypovalves of eighth sternum deep, ventral margin curved upward, dorsal margin nearly straight (Fig. 216). Arms of genital furca slender apically, slightly widened near base (Fig. 217); basal portion more than twice as long as wide. Ninth sternum a strongly sclerotized, broad, transverse band narrowed abruptly and bent cephalad at each side (Fig. 217). Cerci about 4.5 times as long as greatest width, straight in basal one-third or more, then evenly upcurved both dorsally and ventrally, subequal in length to hypovalves or slightly longer.

Types.—Holotype, male, near the Continental Divide, Boulder Co., Colorado, elevation 9800 ft, 17 April 1952, William S. Osburn collector. Allotype, female,



Figs. 213-218, *Chionea nigra.* 213, left antenna, male paratype, approximately dorsal aspect (slide-mounted). 214, details of ninth abdominal segment, male, dorsal aspect (left basistyle and dististyle and base of ninth segment omitted; tenth segment pushed inward to expose gonapophyses). 215, left dististyle and apex of basistyle, male from Utah, posteroventral aspect. 216, terminal abdominal segments, female, left lateral aspect. 217, ninth sternum and genital furca, ventral aspect. 218, same, left lateral aspect. Scales: a—213-215, 217-218; b—216.

same data as holotype except elevation 9500-11,000 ft and date 24 April 1952. Paratypes (essentially topotypic), all from near the Continental Divide, Boulder Co., Colorado: 1 ♂, 1 ♀, same data as allotype; 3 ♂, 1 ♀, 9600-9900 ft, 27 February 1953; 1 ♂, 9500 ft, 7 March 1953; 2 ♀, elevation not recorded, 20 March 1953; 1 ♂, 9800 ft, 31 March 1953; 1 ♂, 2 ♀, 10,000 ft, 8 April 1952; 1 ♀, 7 mi W of Nederland, 9500 ft, 10 April 1953; 1 ♀, 11,200 ft, 28 April 1953; 2 ♀, 11,300 ft, 26 October 1951; 1 ♂, 11,400 ft, 3 November 1951; 1 ♀, 1 ♀, 8 mi W of Ward, 11,400 ft, 10 November 1951; all collected by W. S. Osburn; 1 ♀, 1 mi N Nederland, 8500 ft, 27 Dec. 1970, G. W. Byers. Most of these specimens were taken on the high slopes above the Univ. of Colorado Mountain Research Station ("University of Colorado Camp" on some maps), about 14 mi W of Boulder. Additional paratypes: COLORADO, Larimer Co., 1 mi. NE of Cameron Pass, 9600 ft, 5 Feb. 1966, S. G. Wellso (1 ♂); Routt Co., Clark (on Elk River), on snow, 10 Jan. 1978, T. Marchell (1 ♂); San Miguel Co., Wilson Mountain, Telluride, on snow, 29 Dec. 1977, T. B. Smith (1 ♀). UTAH: Cache Co., Logan Canyon, Beaver Mountain, 28 Oct. 1963, R. Rust (1 ♂); Summit Co., Henrys Fork C. G. (campground?), Uinta Mountains, 20 Dec. 1975, R. Fort (1 ♂). Holotype, allotype, two male, three female paratypes, all pinned, and three male, three female paratypes, in alcohol, in the collection of the Univ. of Colorado Museum, Boulder, Colorado. Other paratypes are in the collections of the Univ. of Michigan, Univ. of Kansas, Colorado State Univ., Utah State Univ., Univ. of Wisconsin, and Cornell Univ. Two females from Rocky Mountain Biological Laboratory, Gunnison Co., Colorado, collected in winter 1980 by Sara Hiebert, have not been made paratypes.

Variation.—The usual number of flagellar segments is three, and where there is only one beyond the fusion segment it is clearly the result of fusion of two segments, there being the usual three terminal hairs as well as the dorsal and ventral hairs of the subapical segment, all on one rather elongate segment. Occasionally the fusion segment is narrowed apically, giving the appearance of an additional segment, and rarely this part actually becomes articulated with the fusion segment, resulting in four flagellar segments. The femoral setae vary in size, the smaller ones generally found in the dorsolateral and ventrolateral rows. The larger setae in males usually have attenuate, curved tips. Specimens preserved in alcohol appear a little lighter in color than those that are dried, the females especially having a dark brownish color, except for the head, which is black.

Relationships.—A member of the *alexandriana* group, *Chionea nigra* is most like *alexandriana* itself and may well be a geographically isolated derivative of that species. Males of *nigra* closely resemble those of *alexandriana* and *jellisoni* in most structural details that ordinarily are taxonomically useful, such as the shapes of the gonapophyses, diststyles, and ninth abdominal tergum, and the number of antennal segments. The ventral process on the hook of the gonapophysis is somewhat less prominent in *nigra,* but color, in this case, appears to be the easiest means of distinguishing the species. In females, also, the black color will differentiate *nigra* from all other species, and the short, evenly curved cerci and smoothly margined ninth sternum of *nigra* will serve further to distinguish this species from *alexandriana.* The specific name refers to species' overall black color.

Geographic Distribution.—*Chionea nigra* is so far known only from scattered localities at high elevations in Colorado and Utah (Map 8). This distribution does not present a very coherent pattern and clearly is fragmentary. The range of the species may be cut off to the north by the high, dry plains of southern Wyoming, and the record from San Miguel Co., Colorado, is probably near the southern limit of the range. The specimens from Routt Co., Colorado, and Summit Co., Utah, supply only a tenuous connection to the Wasatch Range of central Utah, where *nigra* contacts the similar *C. jellisoni.*

Seasonal Distribution.—There are plainly two separate periods of occurrence of adults on the snow in the type locality, one in October and November, the other in late February, March and April. Since Osburn's study of the area was continuous and since he was watching for *Chionea* particularly during the entire 1952-1953 season, I believe that the interval between these peaks is actually a time when adults of *Chionea* are not present and that the peaks may represent two generations.

Habitats.—I am indebted to Mr. Osburn for several very useful observations on the environments in which this species occurs and for searching beyond the areas in which the insects were found, so that the pattern of ecological distribution was made clear. *Chionea nigra* was collected on 12 different dates in three years. In every instance the specimens were found on snow, although the extent of the snow cover varied from shallow and patchy in distribution to deep and completely covering the ground, the condition of the snow from freshly fallen and soft to several days old, with an icy crust at the surface. Collections made between 9500 and 11,200 ft elevation were in lodgepole pine (*Pinus contorta*) forest, except where as a result of fire these trees had been temporarily replaced by aspen, or, in one case, limber pine. Above 11,200 ft the forest is spruce (*Picea engelmanni*) and fir (*Abies lasiocarpa*) to timberline, which is near 11,500 ft in that vicinity. *Chionea nigra* was never found more than 100 ft from trees projecting above the snow level, while a species of *Boreus* often found in association with the tipulids was taken as high as 700 vertical feet above timberline (see Byers, 1955: 4). Four of the 12 collections, comprising nearly half the specimens, were made when the temperature was between 18°F (–7°C) and 29°F, the others at temperatures from 32-40°F (5°C). Most of the Chioneas were taken late in the day, a few at sunset or after nightfall, and some were found only after a prolonged search, suggesting the insects were coming out onto the snow surface as the light intensity was diminishing. Two were collected at 10:00 A.M. but on a day when the sky was completely overcast, and one was taken at 2:30 P.M. when there was a nearly complete cloud cover.

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APPENDIX 1

Chionea wilsoni, NEW SPECIES

(see p. 142)

Diagnosis.—A generally yellowish, southern Appalachian species with long antennae having 10-11 flagellomeres; male gonapophyses inwardly and downwardly inclined, flattened blades with narrowly rounded apices; dististyles spatulate with mesal concavity in apical half; female cerci long, slender but slightly widened subapically; abdominal terga with distinct brownish markings.

Description (based on 6♂, 4♀, preserved in alcohol).—General appearance: Head yellowish brown to brown, thorax yellowish brown, palest dorsally; abdominal terga yellowish brown distinctly patterned with brownish lateral borders and median spot, sterna pale yellowish brown narrowly darkened with brown at sides; pleural membrane pale grayish yellow. Length of male, exclusive of antennae, about 3.1-5.2 mm (holotype 5.2 mm), female 4.0-5.8 mm (allotype 5.1 mm).

Head: Antennae (Fig. 219) with pedicel longer than cylindrical scape; number of flagellomeres usually 11, the first (fusion segment) subconical, about 1.5 times as long as its basal diameter; antennal length, holotype, 1.72 mm. Clypeus and maxillary palps brown. Setae of vertex mostly long, dark, slightly curved. Eyes with about 90-110 ommatidia each.

Thorax: Thoracic dorsum pale grayish yellow to yellowish in central area, grading into brown laterally, darkest on anterior edge of pronotum and around anterior spiracles. Halteres grayish yellow to pale yellowish brown, not contrasting noticeably with color of nota. Mesonotal setae in two uneven longitudinal rows of 3-4 larger setae; a few smaller hairs. Legs yellowish to yellowish brown; femora with six rows of long, slender, dark setae; tibial setae about as long as those of femora; basitarsi yellowish brown grading into brown in apical one-fifth, other tarsomeres dark brown to nearly black.

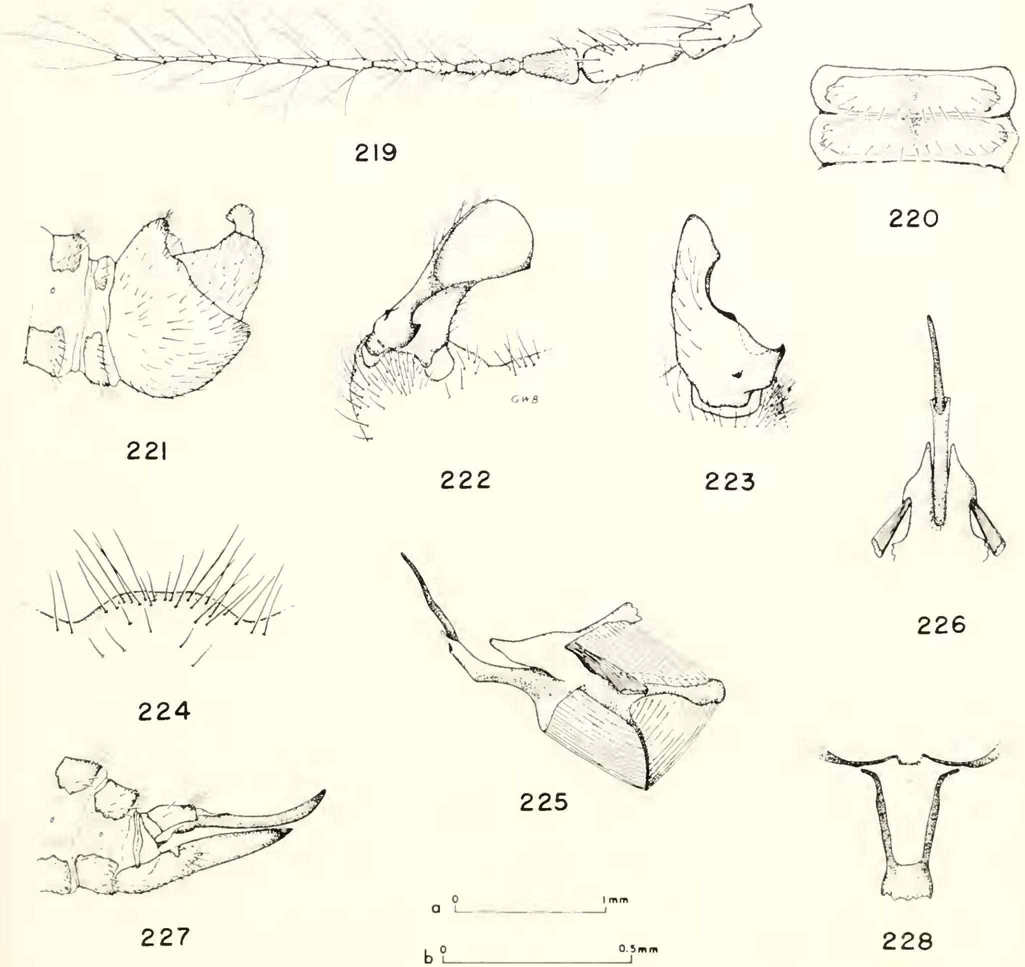
Abdomen of male: Posterior median margin of ninth tergum (Figs. 221, 224) entire or shallowly indented medially in anterodorsal aspect, narrowly notched at mid-line in dorsal aspect, projecting dorsad and caudad, bearing numerous long, slender setae. Gonapophyses (Figs. 225, 226) flattened blades, steeply inclined, dorsal edges about three times as far apart as ventral edges, somewhat thickened at base, each roughly triangular, narrowing posteriorly to acutely rounded apex. Penis with angular deflection dorsad shortly before mid-length, bearing small, finger-like appendage at each side just beyond mid-length; apex unmodified. Posteromesal lobes of basistyles (Figs. 222, 223) scarcely evident, evenly rounded, bearing numerous hairs. Dististyles (Figs. 222, 223) dark yellowish brown, spatulate, with large mesal concavity in apical half, with broadly rounded apex and small, darkened subapical tooth on anterior margin; mesal tooth prominent, darkly sclerotized, slightly upcurved, with small concavity above its base on dorsal surface; ventral tooth a small, rounded protuberance, only slightly darkened. Tenth segment pale yellowish gray, not projecting far beyond ninth tergum, abruptly narrowed near mid-length. Most abdominal terga pale yellowish brown conspicuously patterned with brown median spot and lateral margins (Fig. 220); setae submarginal along posterior edge and sides.

Abdomen of female: Eighth tergum short, or slender, throughout, slightly expanded at each side to about one-fourth length of seventh tergum, without setae, yellowish brown with transverse reddish brown, more densely sclerotized stripe connecting lateral apices (Fig. 227). Hypovalves of eighth sternum elongate, their ventral margins nearly straight, dorsal margins evenly downcurved to acutely rounded apex; margins amber-brown, central area pale yellowish brown, translucent. Arms of genital furca (Fig. 228) not conspicuously bowed, narrowed and curved abruptly outward in apical one-fifth of their length; basal portion wider than long, weakly sclerotized medially. Each side of ninth sternum slender, tapering toward midline to join moderately sclerotized, subtriangular median structure protruding ventrally. Cerci long, slender, slightly widened before acute apex, about nine times as long as their greatest width, approximately 1.3 times as long as hypovalves measured from notch to tip. Setae of terga 6 and 7 neither thicker nor darker than those of more anterior terga.

Types.—Holotype, male, Calhoun Co., Alabama (T14S, R9E, Sect. 17), 11 December 1980, elev. about 1200 ft, collected by Dr. Cole L. B. Benton. Allotype, female, topotypic, 5 Dec. 1980. Paratypes, all collected by Cole Benton and all from northeastern Alabama: 1 ♂, Calhoun Co., along road by Camp Cottaquilla, T14S, R9E, Sect. 32, about 900 ft, 31 Dec. 1980; 4 ♂, same locality, 26 Jan. 1981; 1 ♀, topotypic except Sect. 18, about 1200 ft, 6 Dec. 1980; 1 ♀, Cherokee Co., Little River Canyon rim (west side), near stream by Powell Trail, 21 Dec. 1980; 1 ♀, Talladega Co., Talladega National Forest, Mump Creek at road between Ironaton and Clairmont Gap, 2 Jan. 1981.

Holotype and allotype in the Snow Entomological Museum, University of Kansas; paratypes returned to Dr. Benton, who plans to deposit some in the collection of the Ohio State University, Columbus.

At the suggestion of the collector, Dr. Benton, this striking new species is named in honor of Prof. Edward O. Wilson of Harvard University. This recognizes Prof. Wilson's great contributions in theoretical biology (sociobiology in particular) and in myrmecology, and that he was born and



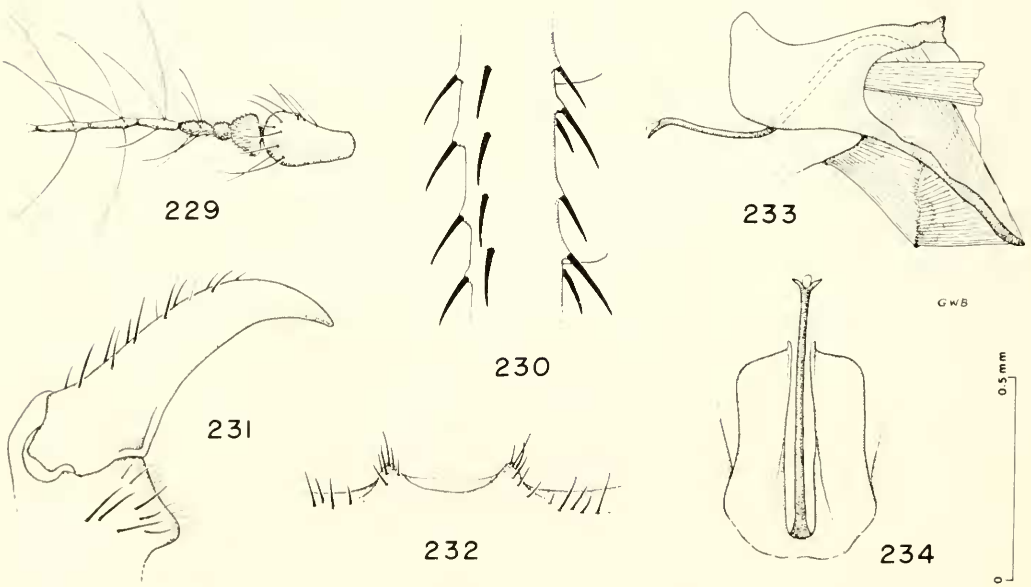
Figs. 219-228, *Chionea wilsoni*. 219, left antenna, male holotype, left lateral aspect. 220, abdominal terga 3, 4, dorsal aspect (anterior at top), to show color pattern. 221, terminal abdominal segments, holotype, left lateral aspect. 222, left dististyle and apex of basistyle, paratype, mesal aspect. 223, left dististyle and apex of basistyle, holotype, posterior aspect. 224, median portion of ninth abdominal tergum, male paratype, anterodorsal aspect. 225, right gonapophysis, penis, vesica and associated apodemes and muscles, right lateral aspect. 226, gonapophyses and penis, dorsal aspect. 227, terminal abdominal segments, female allotype, left lateral aspect. 228, ninth sternum and genital furca, female paratype, posteroventral aspect. Scales: a—220-221, 227; b—219, 222-226, 228.

raised in Alabama. It further recognizes my own 27-year friendship with him.

Variation.—Size variation in *C. wilsoni* is considerable for the small number of individuals available; this is especially noticeable in males. In some specimens, the darker brown lateral borders of the abdominal terga are connected across the anterior margin of each tergum; also some of the median tergal spots are a little diffuse in certain individuals. The femora of the males are not greatly incrasstae, even in the holotype which is the most robust of the series at hand. The extent to which the ninth abdominal tergum of the male is produced dorsad (or upward and backward) varies; Figure 224 shows the least projection of this mid-tergal region in any of the males available. Variation in the number of flagellomeres beyond the fusion segment has been mentioned earlier.

Relationships.—Antennal structure, body color, the shapes of the gonapophyses and ninth abdominal tergum in the male, and shapes of cerci and hypovalves in the female all indicate *Chionea wilsoni* belongs to the *scita* group. Within this species group, it most nearly resembles *C. scita*, and its geographical position suggests it may have been derived from *scita* (Map 1). From all other members of the *scita* group, males of *wilsoni* may at once be differentiated by the unique dististyles. Both males and females may be recognized by their tergal color pattern (the characteristic by means of which the female from northern Georgia was determined to be *scita* and not *wilsoni*).

Geographic Distribution.—The range of *C. wilsoni* is probably limited to the extreme southwestern Appalachian Mountains of northeastern Alabama and possibly adjacent Georgia (Map 1). Records of Chioneas belonging to the *scita* group from northeastern Georgia and further north in the Appalachians apparently all pertain to typical *scita*. Although this is the southern-



FIGS. 229-234, *Chionea macnabeana*, male. 229, pedicel and base of flagellum, right antenna, mesal aspect. 230, portion of hind tibia, near mid-length, mesal aspect. 231, left dististyle and apex of basistyle, posteroventral aspect. 232, median portion of ninth abdominal tergum, anterodorsal aspect. 233, right gonapophysis, penis, vesica and associated apodemes and muscles, right lateral aspect. 234, gonapophyses and penis, dorsal aspect. Scale: all figures.

most range for the genus (near 33°30′ to 34°N) it can still be considered essentially montane (elevations near 275-370 m, or 900-1200 ft) and cold in winter.

Seasonal Distribution.—A single early-winter generation is indicated by the available collection data. All records are for early December to late January, the coldest time of the year in mountainous northeastern Alabama.

Habitats.—All known specimens of *Chionea wilsoni* were found in leaf litter, from which they were extracted by sifting or by Berlese funnel. The forest in the type locality is the oak-hickory-pine association that is widespread at middle elevations of the southern Appalachian Mountains. In fact, with respect to climate, physiography and forest cover, the habitat of *C. wilsoni* is much the same as that for the southern Appalachian part of the range of *C. scita*.

APPENDIX 2

MALE OF **Chionea macnabeana** ALEXANDER

(see p. 132)

Abdomen of male.—Posterodorsal margin of ninth tergum (Fig. 232) with broadly U-shaped median emargination wider than deep; at each side of emargination a short, thick lobe bearing 4 or 5 stout black setae. Gonapophyses (Figs. 233, 234) appearing broad in both dorsal and lateral aspects, mesal surfaces approximately vertical, joining dorsal surfaces at nearly right angle; color generally dark yellowish brown, posterior vertical margins thin, hyaline. Penis downcurved from base, its apex divided into two acuminate points, one at either side of nearly transparent terminal vesicle (endophallus?). Posteromesal lobe of basistyle (Fig. 231) subquadrate, strongly sclerotized and darkened, with yellowish hairs on inner (dorsal) surface. Dististyles brown, narrowing and curving evenly from base to acute apex (Fig. 231); setae on outer curvature sparse, mostly thick and black, but some more hair-like; mesal tooth inconspicuous, darkly sclerotized but low and rounded; no ventral tooth. Tenth segment (proctiger) grayish, not abruptly narrowed near mid-length. Abdominal terga unevenly yellowish brown to brown, without pattern; 4-6 thick, black setae along posterior edge of each; additional group of stout, black setae at posterolateral corners of terga 6-8.